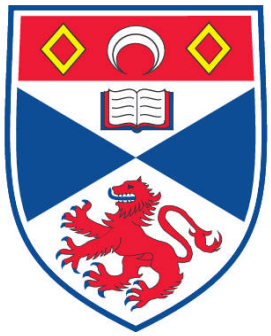
ATTENTION FOLLOWING AND NONVERBAL REFERENTIAL COMMUNICATION IN BONOBOS (*PAN PANISCUS*), CHIMPANZEES (*PAN TROGLODYTES*) AND ORANGUTANS (*PONGO PYGMAEUS*)

Elainie Alenkær Madsen

A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews



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DECLARATION

I, Elainie Alenkær Madsen, hereby certify that this thesis, which is approximately 67,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in November 2004 and as a candidate for the degree of Ph.D. in August 2006; the higher study for which this is a record was
carried out in the University of St Andrews between 2004 and 2009.

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ABSTRACT

A central issue in the study of primate communication is the extent to which individuals adjust their behaviour to the attention and signals of others, and manipulate others' attention to communicate about external events. I investigated whether 13 chimpanzees (*Pan troglodytes spp.*), 11 bonobos (*Pan paniscus*), and 7 orangutans (*Pongo pygmaeus pygmaeus*) followed conspecific attention and led others to distal locations. Individuals were presented with a novel stimulus, to test if they would lead a conspecific to detect it in two experimental conditions. In one the conspecific faced the communicator, while another required the communicator to first attract the attention of a conspecific. All species followed conspecific attention, but only bonobos in conditions that required geometric attention following and that the communicator first attract the conspecific's attention. There was a clear trend for the chimpanzees to selectively produce a stimulus directional 'hunching' posture when viewing the stimulus in the presence of a conspecific rather than alone (the comparison was statistically non-significant, but very closely approached significance [$p = 0.056$]), and the behaviour consistently led conspecifics to look towards the stimulus. An observational study showed that 'hunching' only occurred in the context of attention following. Some chimpanzees and bonobos consistently and selectively combined functionally different behaviours (consisting of sequential auditory-stimulus-directional-behaviours), when viewing the stimulus in the presence of a non-attentive conspecific, although at species level this did not yield significant effects. While the design did not eliminate the possibility of a social referencing motive ("look and help me decide how to respond"), the coupling of auditory cues followed by directional cues towards a novel object, is consistent with a declarative and social referential interpretation of non-verbal deixis. An exploratory study, which applied the 'Social Attention Hypothesis' (that individuals accord and receive attention as a function of dominance) to attention following, showed that chimpanzees were more likely to follow the attention of the dominant individual. Overall, the results suggest that the paucity of observed referential behaviours in apes may owe to the inconspicuousness and multi-faceted nature of the behaviours.

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CHAPTER 1: Introduction

1.1. Evolutionary perspectives

1.1.1 Communication and language

Contemporary models of hominid cognitive evolution and almost all formulations of the gestural theory of language origins have emphasized the importance of the capacity to monitor and manipulate social attention (e.g., Condillac 1728, cited by Hewes 1981; Corballis 2002). The story of the evolution of language, however, overlaps with the story of the evolution of communication. Despite many and varied theories of human language origins, it seems clear that language did not appear fully-formed by virtue of a macro-mutation (e.g., Bickerton 1990, cited by Bickerton 2003), but emerged over an extended period of evolutionary time, and required a series of mutational changes. Still, speculations about the evolutionary origin of language and its possible precursors in animal communication systems remain controversial. Evidence of an evolutionary timeline for the emergence of capacities that paved the way for fluent language has been sought within a number of disciplines.

1.1.2 Anthropology & neuroanatomy

Much can be deduced about the lives of early hominids from their artefacts and fossils. Ancestral humans walked upright 3.6-3.75 million years ago (m.y.a.), and manufactured and used stone tools 2.6 m.y.a., and fire 400 thousands year ago (k.y.a.) (Leakey & Hay 1979; Brain & Sillent 1988; Semaw 2000). Moreover, anthropological studies have pinpointed the emergence of the only undeniable physical evidence of language, writing, to 6 k.y.a. While such physical evidence allows us to deduce an evolutionary timeline for the appearance of many distinctive human behaviours, the techniques are of limited use in determining the timing and *earliest* forms of language.

Endocasts of fossil skulls reveal traces on the bone left by the surface structure of the brain, and may thereby elucidate the association of brain structures and particular cognitive and communicative skills across extinct as extant species. It is well established that in humans, language comprehension and production are lateralised in particular regions within the left hemisphere, and that non-speech, gestural communication systems are controlled by the same areas (see e.g., Corballis 2002). Cranial endocasts of *Homo habilis* fossils reveal an enlarged Broca's area in the left hemisphere (associated with fine oro-facial motor control and speech production), suggesting that neuro-anatomical changes associated with speech production had appeared by 1.6 m.y.a. (e.g., Ambrose 2001). In primates, vocalisations with a strong negative emotional valence appear to show a *right* hemisphere asymmetry (Hook-Costigan & Rogers 1998, cited by Hopkins & Cantero 2003), which is consistent with the traditional interpretation that non-human primate vocalisations convey affective, rather than semantic and symbolic information. There are, however, many reports of *left* hemisphere dominance in non-human animals' processing of species-specific sounds, and chimpanzees, bonobos and gorillas, have a structure (Brodmann's area 44) that resembles Broca's area and exhibits a similar left-hemisphere dominance (Cantalupo & Hopkins 2001).[1] In chimpanzees, this Broca's homologue is activated during communicative gestural and vocal signaling (Taglialatela *et al.* 2008), and chimpanzees (particularly those raised by humans), preferentially use the right hand (controlled by the left hemisphere) in gestural food begging contexts, and are more likely to use right hand gestures when accompanying them with a vocalisation (Hopkins & Cantero 2003). Given a Broca's homologue in non-human apes (who do not possess fully-fledged language), the mere presence of an enlarged Broca's area in *Homo habilis* fossils represents a necessary, yet not sufficient, condition for inferring modern language abilities. While fossil craniums represent the only direct evidence of the morphology of ancestral hominoid brains, they are thus of limited use in creating an evolutionary timeline for cognitive and communicative abilities, given the tenuous correlation between anatomical surface structure and their functions. Overall, however, these findings suggest that some of the neurological bases for intentional vocal and gestural communication were present in the last common ancestor of humans and non-human apes.

[1] Schenker and colleagues (Schenker *et al.* 2010), however, report contradictory results, and that although some chimpanzees have asymmetrical Broca's areas (i.e., >10 % difference in the number or volume of neurons in the left and right hemispheres), there was no clear evidence of a group-wide Broca's asymmetry across the chimpanzees they examined. The jury is thus somewhat 'out' with respect to homologous Broca's asymmetries in non-human apes.

The characteristically descended larynx in the throats of adult humans has played a central role in theories about the evolution of speech (e.g., Diamond 1991), as it provides a sound-modifying space that allows a larger range of sounds to be produced faster than those in species with a high positioned larynx (e.g., Lieberman 2007). Recent findings that chimpanzees' larynxes and hyoids bones (as those of modern humans), descend during infancy and the early juvenile period (Nishimura *et al.* 2003, 2006), however, suggest that the phenomenon is not unique to humans, and that this morphological foundation for speech evolved in a common ancestor of extant hominoids.

1.1.3 Genetic markers

The discovery of a gene implicated in the processing and articulation of speech has narrowed the timeframe for the emergence of fully-fledged human language. Study of three generations of a large British family (KE) with heritable linguistic and grammatical impairments (Hurst *et al.* 1990) has uncovered the significance of FOXP2, a gene involved in grammar comprehension, sentence construction and the sequencing of oro-facial movement for fluent speech articulation (Lai *et al.* 2001). Based on the monomorphism of low-frequency alleles in the region around the FOXP2 gene across extant human populations (which is suggestive of genetic hitchhiking and reduction of variation as a result of strong positive selection), Enard and colleagues (Enard *et al.* 2002) dated the human FOXP2 to the emergence of anatomically modern humans, less than 200 k.y.a. Recent evidence that two Neanderthal remains carry the human variant of FOXP2, extended the evolutionary timeline, and suggested that the variant emerged in the last common ancestor of humans and Neanderthals, at least 400 k.y.a., only to become uniform, fixed and widespread in *Homo sapiens*, within the last 200 k.y.a. (Krause *et al.* 2007). The protein made by human FOXP2 shows almost no variation across vertebrates, and has changed by only three amino-acids (of a total 715) since primates diverged from the line leading to extant mice 130 m.y.a. Two of the mutations, however, emerged in the 5-7 million years after the human lineage separated from the ancestor shared with chimpanzees and bonobos, suggesting that human FOXP2 evolved recently and rapidly, and by implication, conferred a significant evolutionary advantage (Enard *et al.* 2002). There is thus a strong case for the argument that the two amino-acid substitutions were under positive selection by virtue of, possibly, their role in language.

The human FOXP2 variant is, however, not a linguistic Rubicon, and neither a necessary, nor sufficient condition for spoken language. Despite burial rites, a human-like hyoid

bone (connecting the larynx and tongue), and the potential for a flexibly, descendible larynx[2] in Neanderthals, the high mortality rate and paucity of symbolic expression and technological progress suggest that Neanderthals lacked modern human speech capacities. Likewise, despite a modern FOXP2 and some fossil evidence of a physiological capacity for speech in anatomically modern humans between 100-200 k.y.a., the lack of creative artifacts until about 50 k.y.a. implies an absence of some essential aspect of communication. FOXP2 may, however, have implications beyond spoken language. The gene regulates the expression of other genes, activating some while suppressing others, and triggers a cascade of changes in genes affecting brain development (Vernes *et al.* 2008). It drives genes to behave differently in humans and chimpanzees (Konopka *et al.* 2009)[3], and, intriguingly, in humans, down-regulates a gene (CNTNAP2) involved in autism (Alarcón *et al.* 2008), a condition affecting a suite of communicative and cooperative skills related to joint attention, and the ability to form a theory of mind.

1.2 Non-human primates

1.2.1 Behaviour and genetics

While the fossil record and comparison of the languages of modern humans inform theories about the emergence of the modern human mind and language, they provide limited evidence as to the cognitive and communicative skills of ancestral hominids prior to the recent evolution of the *Homo* line. Recent disclosure of analysis of one of the earliest 4.4 million old hominid fossils, *Ardipithecus ramidus* (ARA-VP-6/500), has emphasized differences in the behaviour and social structure of early hominids and modern non-human apes, and that e.g., humans and chimpanzees evolved along different paths. While the implication is that modern apes are poor proxies for characterizing hominid evolution (White *et al.* 2009) (as they are, naturally, referential models and not *representatives* of human ancestors), considerable evidence of ape behaviours that reflect those of extinct as extant humans (aimed throwing, spatial cognition

[2] Demonstrations that the larynges of red and fallow deer (*Cerrus elaphus* & *Dama dama*), can flexibly descend during roaring (Fitch & Reby 2001), opens the possibility for a similar modifiability in other species, such as Neanderthals, which would have provided such species with a larger and more flexible range of sounds than traditionally attributed to them.

[3] While Konopka *et al.* (2009) showed that human and chimpanzee FOXP2 variants have different expressions in *in vitro* brain tissues, both FOXP2 variants were tested in human brain tissues, thereby allowing for a confound, as e.g., diet affects human and chimpanzee gene expressions (see e.g., Somel *et al.* 2008).

etc.), of which at least some have deep phylogenetic roots within the primate lineage, means that identifying cognitive and communicative homologies, as well as analogies and differences of modern humans and extant non-human primates *can* inform hypotheses about the social and mental lives our last common ancestor. Indeed, comparison of the natural communication systems of humans and other primates can help identify which specific capacities were present in our last common ancestor, and how they may have been deployed.

The study of communication and cognition of extant primates has centered on the great apes, as they constitute the most recent evolutionary divergence from the human lineage. Orangutans (*Pongo pygmaeus* and *Pongo abelii*) separated from the human lineage 10-12 m.y.a. (Stauffer *et al.* 2001), gorillas (*Gorilla gorilla* and *Gorilla beringei*) 7-9 m.y.a., and chimpanzees (*Pan troglodytes* and *Pan paniscus*) approx. 6 m.y.a. While fossil evidence of bipedalism inferred from the Toumaï cranium (*Sahelanthropus tchadensis*, one of the earliest dated human fossils), indicates a human-chimpanzee divergence of 6.5-7.4 m.y.a., differences in nuclear DNA protein coding genes (Kumar *et al.* 2005) and base pairs (Patterson *et al.* 2006) lead to estimations of 5-7 m.y.a. and less than 6.3 m.y.a., respectively. Human and great ape genetic similarity correspond to the duration of shared ancestry. While the average genome-wide DNA sequence difference between humans and other apes vary with as little as 1.2 % (chimpanzees), 3 % (gorillas) and 7 % (orangutans; King & Wilson 1975; Wildman *et al.* 2003), about 15 % of all genes have changed their expression level in at least one region of the brains of humans and chimpanzees (Pääbo 2003), suggesting a possible non-linear and cascading expression effect of small genetic differences.

Recent claims of episodic-like memory (Clayton & Dickinson 1998), planning (Raby *et al.* 2007), alliance formation (Emery *et al.* 2007), post-conflict third party affiliation (Seed *et al.* 2006), and functional awareness of what others have seen in birds (Dally *et al.* 2006), demonstrate that behavioural complexity is by no means limited to primates[4]. Nonetheless, apes distinguish themselves from other species through their genetic proximity as much as cognitive affinity to humans.

[4] Rudimentary syntactical abilities, conceptual semantics and referential labeling have also been demonstrated in the auditory communication systems of a number of monkey species (Zuberbühler *et al.* 1999; Zuberbühler 2000; Arnold & Zuberbühler 2008; Ouattara *et al.* 2009).

1.2.2 Smoke and Mirrors

While monkeys and lesser apes react to their mirror reflection with hostility or affection, as if a conspecific (e.g., capuchins, *Cebus apella*: Anderson & Roeder 1989; de Waal *et al.* 2005; Roma *et al.* 2007; cotton-top tamarins, *Saguinus oedipus*: Hauser *et al.* 2001, though see Hauser *et al.* 1995 for non-reproducible positive findings; gibbons, *Hylobatidae spp.*: Suddendorf & Collier-Baker 2009; macaques, *Macaca mulatta*: Gallup *et al.* 1980; marmosets, *Callithrix jacchus:* Heschel & Burkart 2006), current consensus is that all great apes species (although by no means every individual) connect their mirror reflections with themselves. Chimpanzees (Povinelli *et al.* 1993; de Veer *et al.* 2002; Bard *et al.* 2006) and orangutans (Suarez & Gallup 1981) pass the 'mirror test', in which subjects are covertly marked with a transparent and coloured dye spot on locations visible only with mirror assistance, and selectively inspect the coloured spot. Most studies have failed to produce convincing evidence of mirror self-recognition (MSR) in gorillas (despite efforts to eliminate methodological issues, such as avoidance of prolonged eye contact, argued by some researchers to represent a threatening signal in gorillas[5]: Suarez & Gallup 1981; Shillito *et al.* 1999), and studies with positive results have failed to include key control measures (e.g., anastesia and the sham-mark control condition: Posada & Colell 2007). Nonetheless, there is evidence that two gorillas with extensive human experience pass the mark test (Patterson & Cohn 1994; Allen & Schwartz 2008). While all studies of bonobos have lacked important controls (e.g., the experimental mark and sham-mark procedure: Westergaard & Hyatt 1994; Walraven *et al.* 1995; Inoue-Nakamura 1997), bonobos show evidence of mirror-mediated self-exploration. Overall, these results suggest that MSR emerged in the great apes by virtue of common descent, after the split from the line leading to the lesser apes 14 m.y.a. Some suggestion of MSR in one dolphin, *Tursiops truncatus* (Reiss & Marino 2001; Sarko *et al.* 2002) and two of eight elephants tested (*Elephas maximus*, Povinelli 1989; Simonet 2000, cited by Nissani *et al.* 2007; Plotnik *et al.* 2006; Nissani *et al.* 2007)[6] suggest that the skill may also arise in multiple taxonomic groups by means of convergent evolution. Interestingly, compelling evidence of MSR in corvids (two magpies, *Pica pica*: Prior *et al.* 2008; see also Thompson & Contie 1994 for non-reproducible positive findings in pigeons by Epstein *et al.* 1981) suggests that a neocortex (of which birds have none) is not a requirement for MSR.

[5] Eye contact has been argued by some researchers (e.g., Shillito *et al.* 1999) been claimed to represent a threatening signal in gorillas, yet there seem little evidence in support of this claim.

[6] While elephants (Povinelli 1989; and pigs: Broom *et al.* 2009) can use mirrors to guide their own reaching behaviour, only two of eight elephants tested passed the mark test. More than 50% of chimpanzees tested, however, also fail the mark test, and the low proportion of elephant passes may be partly due to the limited number of subjects.

The exact significance of the MSR species differences remains to be elucidated, however, there is some evidence that MSR may be underpinned by the same skills as imitation recognition, which shows a similar dissociation across monkeys and apes, and is considered to engender a concept of self as different from others. While macaques recognise when imitated (i.e., show increased attention to experimenters who mirror their actions: Paukner *et al.* 2005), they do not, unlike apes (Nielsen *et al.* 2005; Haun & Call 2008), show *explicit* signs of imitation recognition (i.e., engage in so-called 'testing behaviours'). The implicit imitation recognition by macaques may be akin to what de Waal and colleagues (de Waal *et al.* 2005) have termed the mental category of 'Puzzling Other', to describe the discomfort that capuchins exhibit in response to their mirror reflection, which they seem to understand is no stranger.

Whether MSR qualifies as evidence of self-awareness remains controversial (Bard *et al.* 2006). While an initial finding that chimpanzees reared in isolation from conspecifics failed to show MSR (Gallup 1977), linked MSR to a socially engendered self-awareness (Gallup 1977, 1998) that enabled representation of other's mental states (Gallup 1982), MSR has since been demonstrated in chimpanzees raised in a variety of environments. The ability of autistic children, who are unable to make complex social attributions (e.g., Leslie 1987), but nonetheless engage in mirror self-directed behaviours (Spiker & Ricks 1984), and the failure to do so of some Alzheimer patients (who are self-aware: Biringer & Anderson 1993), suggest that the cognitive prerequisites minimally necessary for MSR, were initially overestimated. Indeed, evidence converges to suggest that MSR reflects a kinaesthetic self-concept, allowing individuals to distinguish inputs deriving from their own bodies and elsewhere (e.g., Heyes 1998, p. 105). Individuals may therefore recognise themselves and their own bodies (as evidenced through MSR behaviours) without necessarily recognising that they have a 'mind' (different – as their body - from that of others). The linkage of MSR to non-human theory of mind skills may therefore largely represents a 'red herring'.

1.3 Joint Attention in social cognition

1.3.1 Joint attention

Joint attention is considered the earliest manifestation of inter-subjectivity (the ability to represent others' mental states in some form) and the initial mechanism for individuals to share mental states and experiences and negotiate shared meanings (Baron-Cohen 1995; Tomasello 1995; Scassellati 1999). It is a crucial component for the normal growth of social skills in infants, for whom failure to respond to others' gaze and pointing predicts autism at 18 months of age (Baron-Cohen 1994). Engagement in joint attention is also crucial to, and individual differences predictive of, children's language acquisition and novel word-understanding (Tomasello & Todd 1983; Tomasello & Farrar 1986; Mundy & Gomes 1998), as following a speaker's gaze allows individuals to connect novel sounds to objects, and disambiguate the correct referent among several possible (Baldwin 1995; Brooks & Meltzoff 2005). Moreover, the patterns of attention of experienced individuals allow young ones to learn what is important in the environment, and joint attention is thus integral to social learning, active teaching, and theory of mind (ToM), which develops during joint attentional events (Bruner 1983; Whiten 1991; Tomasello 1999a, 2003). Importantly, joint attention has been cast as an ontogenetic (for children) and evolutionary entry (for the human species) into a world of shared intentionality, where intentions, goals and experiences can be shared, coordinated and directed (Tomasello 2003). Joint attention to outside entities have thus bee en suggested to be a uniquely human form of social interaction (Tomasello 2003, 2008; Tomasello *et al.* 2005)

Joint attention has been diversely characterized as coordinated joint engagement about a third entity (Bakeman & Adamson 1984), shared attention (Adamson & Bakeman 1991), a form of secondary inter-subjectivity (Trevarthen & Aitken 2001), and intentional co-orientation towards a common focus (Leavens & Racine 2009). Critically, joint attention differs from parallel attention, in which co-focus arises from a series of independent, stimulus-driven events, and from passive joint attention (Bakeman & Adamson 1984), in which one individual has little or no awareness of the other's involvement or even presence. Thus, while attention following, and the more narrow term, *gaze* following (defined as "looking where someone else is looking": Butterworth 1991, p. 223), are critical components of the suite of behaviours that collectively comprise joint attention *mechanisms*, they do not independently constitute joint attention, as they do not necessarily entail that individuals are aware, that they are attending to

the same external thing (Astington 1993; Tomasello 1995).[7] Joint attention requires not only that individuals attend to each others' attentional states, but that they do so in a particular way, and understand that another's attentional state is object-directed, and therefore '*about*' the object (Gómez *et al.* 1993; Gómez 1998; Tomasello 2001). This entails that individuals not only respond to each other's behaviour, but the underlying intentions. Importantly, joint attention is intentional, and involves at least one individual behaving in a goal-directed manner, so as to make its focus of attention accessible, by way of posture, gaze direction, pointing, and/or gaze alternation between the external locus and interlocutor, and in case of miscommunication, attempts to clarify the communication by persisting and/or elaborating its signaling (Bates *et al.* 1975; Bard 1992; Leavens 2004). This creates a triadic relationship of attentional contact between the individuals that is related to the external phenomenon, thereby allowing individuals to interact about and *through* the phenomenon.

Since attentional states are reflected in publicly available cues (e.g., posture and gaze direction), individuals need, however, not represent the *content* of others' mental states, in order to respond appropriately, or indeed to provoke a potentially predictable set of responses. As Gómez notes, one may "understand other people's minds using first-order representations of behaviours that directly reflect mental states such as attention" (Gómez 1994, p. 72). Gómez and colleagues (Gómez *et al.* 1993) provide an example of a gorilla taking a person's hand and leading the person to a goal (a door to be opened), while the two exchanged looks and gaze towards the goal (the door). This requires, minimally, that individuals associate attentional contact with action and, potentially, a predictable sequence of subsequent behaviours, meaning that higher-order, meta-representational, intentional states are not necessary to attain the behavioural consequences of joint attention.

[7] To minimise terminological confusion, the term joint attention (ought in the general literature and) is here reserved for actively shared attention, while visual co-orientation and gaze following (and the more general term, attention following) are termed joint attention *mechanisms* or *behaviours*.

1.3.2 Joint attention in children

The human adaptation to social interaction is evident in early ontogeny, and the development of joint attention skills follows an extended, mosaic trajectory in infants. Within few hours-to-days of parturition, infants engage in structured, social interactions and basic 'conversational' turn-taking (for a review, see Trevarthan & Aitkin 2001), and (as chimpanzees: Myowa-Yamakoshi *et al.* 2003) show sensitivity to eyes and attentional cues, by e.g., discriminating and preferring faces that engage them in mutual rather than averted gaze (Farroni *et al.* 2002).

Gaze following, and the more complex skill of visual perspective taking, are ontogenetic precedents for joint attention and therefore often a starting point for studies thereof. They are both potential precursors to a ToM, as at least visual perspective taking, minimally, requires a functional understanding that others' visual perspective may differ from one's own.

Gaze following is a crucial, social skill that helps individuals gather information about danger, food locations and social interactions, and coordinate joint attention with others (Tomasello 1999). Following a pioneering study by Scaife and Bruner (1975) there has been considerable debate about the temporal emergence of gaze following skills in infants, although most approximations range from 3-12 months, with a developing level of sophistication that arises from a basic motion-cued tracking mechanism. While indications or precursors of gaze following are manifest from 2 months of age, there is little evidence of reliable gaze following in infants below 6 months (possibly related to poor visual acuity and the development of depth perception, which continues until at least 7 months of age: Arterberry *et al.* 1993, cited by Deák *et al.* 2006). Although newborns show a rudimentary form of gaze following, cued by the direction of eye shifts in (images of) faces (Farroni *et al.* 2003), and 2-6 month olds respond (albeit weakly) to adults' gaze shifts by looking to the same side as the adults (D'Entremont *et al.* 1997; Hood *et al.* 1998; Morales *et al.* 1998; Butterworth & Itakura 2000), this requires specific triggering conditions (such as proximity and continuous infant-directed speech) and largely rely on visual tracking mechanisms that respond to motion cues (Farroni *et al.* 2000)[8]. By around 6 months infants follow gaze to distant targets (Butterworth & Itakura 2000) and consistently so to single targets between 7-9 months (Flom & Pick 2005). However, not until around 9 months of age do infants follow gaze independent of motion cues (i.e., a static head pose suffices: Moore *et al.* 1997), and reliably turn their head to the correct (rather than opposite) side that someone gazes (e.g., Corkum & Moore 1995, 1998).

[8] Motion cues alone are, however, insufficient to shift infants' attention, as gaze shifts in the image of an inverted face fail to trigger gaze following (Farroni *et al.* 2003).

1.3.3 Butterworth's Multiple Mechanism Model

Butterworth and Jarrett's (1991) Multiple Mechanism Model suggests that joint attention in 6-18 months old children is successively mediated by an ecological, geometric and representational mechanism. The ecological mechanism, which operates from 6 months of age, is a primitive form of gaze direction detector, and triggers search in the appropriate direction, which, however, stops at the first target encountered, leaving infants unable to identify which of multiple targets an adult attends to. Towards 12 months of age a geometric mechanism emerges, by which infants can approximate a line between the adult and her gaze referent, and localise targets correctly, even when located behind a distracter object. While infants can infer directionality by 12 months, it is not until about 18 months, with the emergence of the representational mechanism, that they can infer intentionality and follow gaze to targets behind themselves (Butterworth & Jarrett 1991), implying that they can grasp that others may see things they cannot. This timing of Butterworth and Jarrett's representational mechanism is consistent with evidence that 18 month olds represent the goals and intentions of adults attempting, but failing, certain object manipulations (Meltzoff 1995). The mechanism affords some degree of representation of other's mental states, and consequently forms part of a ToM. Empirical data of e.g., the temporal emergence of the different types of gaze following skills are, however, not fully consistent with Butterworth's theory, as infants follow points to peripheral targets, and gaze geometrically, around barriers, by 9 (not 12) months and follow adult gaze to targets behind themselves by 12 (not 18) months (Deák *et al.* 2000; Flom *et al.* 2004).

1.3.4 Baron-Cohen's Modular Mind Reading System

Relatedly, Baron-Cohen (1994) has proposed that "mind-reading" comprises of four modules: the evolutionarily old Intentionality and Eye Direction Detectors (ID and EDD), and the evolutionarily more recent Shared Attention and Theory of Mind Mechanisms (SAM and ToMM). While the Intentionality Detector involves detection of intentional (i.e., animated: Tomasello *et al.* 2005) movement, the Eye Direction Detector allows individuals to detect that presence of eye-like stimuli (as demonstrated by infants' preference for human faces and eyes) and gaze direction (e.g., towards self or something else), though not to *represent* what others attend to. The Shared Attention Mechanism, which begins to operate from 9-14 months of age, connects input from the Intentionality and Eye Direction Detectors, allowing individuals to interpret the *gaze* of others as an *intentional* goal state. While the Eye Detection Detector (e.g., mother sees toy) and Intentionality Detector (e.g., mother wants toy) can each build dyadic

representations (between mother and toy), the Shared Attention Mechanism allows for simple triadic representations, such as 'mother sees that I see the toy'. Such detection of shared attention is foundational to that ability to manipulate others' attention. Thus, while younger children pay attention to either another person (e.g., their mother) *or* an object (e.g., a toy), the interactions of older children are often *triadic* and involve coordinating attention between both objects and other individuals. From 18 months onwards, use of the Shared Attention Mechanism triggers and stimulates the Theory of Mind Mechanism, which interprets the representations formed by the ID, ED, and SAM, and uses these to interpret and predict the behaviours of others with reference to mental states (such as beliefs, thoughts, knowledge and pretense)[9].

While several studies have implicated the orbital and medial frontal cortex in ToM abilities (e.g., Fletcher *et al.* 1995; Baron-Cohen *et al.* 1994), there is little other neuro-physiological evidence that Baron-Cohen's modules exist in localised form in humans, and in a way that differs from other primates, and several contradictory findings exist. Indeed, while autists have attention-shifting difficulties compared to normal children (indicating a difference in a basic attention mechanism), initiate and engage in very little joint attention, and show ToM deficits, autism-spectrum disorders are associated with a number of brain differences, with no specific brain architectural abnormalities that directly that map onto Baron-Cohen's distinctions. Given the lack of evidence of innate architectural modules, Baron-Cohen's account seems most plausible if one allows for the possibility that relevant cells specialise though experience. This would contribute to the apparent socio-cognitive differences of mother-reared and human-reared apes, and lends support to the general notion that experience 'matters'. More specifically, it supports the 'enculturation hypothesis' (Call & Tomasello 1996; see also Bering 2004), which holds that ontogenetic engagement in a human socio-cultural environment (including triadic joint attention episodes, and being treated as an intentional agent, whose attention can be intentionally directed) produces cognitive changes in human-reared great apes more typical of human cognition, than of their own species, thereby affecting how they interpret the behaviour of others (e.g., engage in mental state attribution).

[9] Recently a fifth mechanism, the emphasizing system, which emerges around 14 months, has implicated cognitive and emotional empathy (Baron-Cohen 2005).

1.3.5 Joint attention in non-human animals

Since joint attention is ontogenetically related to language acquisition in humans, and natural language has not been observed in species other than humans, many researchers have argued that joint attention is a species-specific human capacity (e.g., Butterworth, 2003; Povinelli & Davis, 1994; Tomasello, Carpenter, & Liszkowski, 2007). Recent research has, however, shown e.g., joint visual attention is not necessary for word learning in neither typical nor atypical (e.g., autistic) human development (Akhtar & Gernsbacher 2007), suggesting that the language and joint attention can be dissociated. Moreover, there is growing evidence that the developmental precursors for language, such as triadic interactions and other joint attention skills are indeed widely present in non-human primate interactions.

The phylogenetic roots of joint attention has received much research interest in the last two decades. Attention following in non-human animals has been studied using two paradigms; (i) The gaze following/visual co-orientation paradigm, which requires individuals to track others' gaze to distal locations, and (ii) the object-choice paradigm, which requires them to use referential gaze and/or pointing cues provided by informed individuals to locate food hidden in one of several locations.

Visual co-orientation has been reported in a variety of non-human species, including goats, *Capra hircus* (Kaminski *et al.* 2005), dolphins (Tschudin *et al.* 2001; Pack & Herman 2004), quails, *Colinus virginianus* (Jaime *et al.* 2009), and ravens, *Corvus corax* (Bugnyar *et al.* 2004). While the initial study of primate visual co-orientation found no evidence that either prosimians, Old or New World monkeys (macaques, capuchins, lemurs, *Lemur catta*, and squirrel monkeys, *Saimiri sciureus*: Itakura 1996) follow the gaze of humans, later studies have persuasively demonstrated spontaneous following of human gaze to distal locations in Old and New World monkeys (macaques: Anderson & Mitchell 1999; Ferrari *et al.* 2000; Tomasello *et al.* 2001; Goossens *et al.* 2008; capuchins & spider monkeys, *Ateles geoffroyi*: Amici *et al.* 2009), and of the head and gaze orientation of photographs of conspecifics by prosimians and Old World monkeys (lemurs: Shepherd *et al.* 2006; Ruiz *et al.* 2009; Diana monkeys, *Cercopithecus diana diana*: Scerif *et al.* 2004; macaques: Emery *et al.* 1997; Lorincz *et al.* 1999). Gaze following to distal locations by apes has mainly been studied in chimpanzees and orangutans. Chimpanzees brought up with extensive human contact follow the gaze of human experimenters to locations outside their visual fields, checking above and behind themselves, and to the experimenter when attention following leads to no interesting sights (Povinelli & Eddy 1994, 1996a, 1997; Itakura 1996; Call *et al.* 1998; Tomasello *et al.* 2007). While the majority of studies have addressed the

ability to follow the gaze of humans, chimpanzees, soothy mangabeys (*Cercocebus atys trquatus*) and three species of macaques (*Macaca mulatta, Macaca arctoides*, *Macaca nemestrina*) also follow the attention of conspecifics, under conditions where the observed individual has been induced to raise its head to a distinctive 80° angle, to look towards food presented in an observation tower (Tomasello *et al.* 1998, Figure 1.1). In a recent study Pitman and Shumaker (2009) reported that all the great ape species followed the gaze of a human looking towards the ceiling (an experiment modelled on a study by Bräuer *et al.* 2005), and of one or multiple other apes, induced to raise their heads to a location approx. 2m above and immediately behind the subject (i.e., gaze-following individual, an experiment modelled on the study by Tomasello *et al.* 1998).

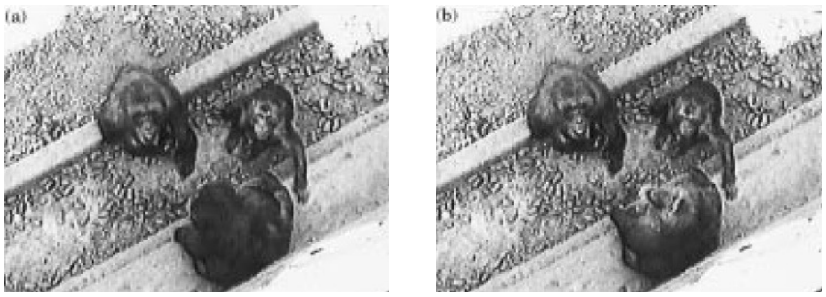

Figure 1.1: Experimental set-up of intraspecific gaze following test of five primate species (images taken from Tomasello *et al.* 1998). (a) The experimenter presents a food item from the location of the camera, in view of two communicators (above, left and right); (b) The target (below) follows the attention of the communicators.

While apes are capable of following human gaze direction independent of head orientation, only 30% (Povinelli & Eddy 1996a) of 'gaze-only' trials conducted with chimpanzees, and 13% of trials in a study of chimpanzees, bonobos and gorillas (Tomasello *et al.* 2007), elicited gaze-following responses to the correct side. Indeed, a comparison of non-human apes' and human infants' gaze following of an experimenter who looked to the ceiling with either 'eyes only', or directed her head towards the ceiling while keeping eyes closed, suggest that while 12 and 18 months old human infants almost exclusively use eye direction in such gaze following situations, chimpanzees, bonobos and gorillas rely primarily on head direction (Tomasello *et al.* 2007). Thus, while humans follow eye gaze from an early ages, non-human apes initially and primarily respond to only head direction, and only later, in adulthood, begin to respond to eye gaze. This human reliance on eye direction, from every early in ontogeny is perhaps not surprising, as compared to non-human primates, humans have particularly conspicuous eyes (Kobayashi & Kohshima 1997), and represent the only primate species to universally have white scelara and a transparent conjunctiva (the membrane covering

the scelara) to contrast a darker coloured iris (thus facilitating detection of visual focus: Kobayashi & Kohshima 2001).

The tendency of humans (in contrast to other apes) to rely predominantly on eye direction lends support to the 'cooperative eye' hypothesis, which posits, that the highly conspicuous eyes of humans evolved under a selective pressure to facilitate close-contact joint attentional episodes and (silent) cooperative communication (during e.g., collaborative hunting), by aiding individuals to follow each others' gaze direction (Tomasello *et al.* 2005, 2007). That is, the hypothesis suggests that adaptations that promote joint attention may have evolved as ancestral humans became more interdependent. While the hypothesis accounts for non-human apes' low reliance on eyes in gaze following contexts, it makes no predictions about their underlying cognitive understanding of other's gaze. Although apes following human attention into empty space may be more inclined to use other indicators of attention, than eye gaze, there is considerable evidence that chimpanzees do recognise eyes as an important indicator of whether a human will respond to their food begging behaviour (Hostetter *et al.* 2007). In contrast to findings by e.g., Povinelli and colleagues (e.g., Povinelli & Eddy 1996a), Hosetter and colleagues have reported that chimpanzees are more likely to precede food begging gestures with a vocalisation, when faced with an experimenter with her eyes closed (versus eyes open), and use more visual gestures when faced with an experimenter with open eyes.

A more demanding test of visual co-orientation than gaze following into empty space (i.e., '*direct* attention following'), consists of blocking an experimenter's line of sight to the target with a barrier, forcing the gaze-follower to choose among several locations, as targets of the other's gaze. The gaze-follower may erroneously look to or past the barrier, and ignore that it blocks the other's view of objects behind it, or correctly follow the other's gaze *geometrically*, by locomoting around the barrier to look to the other's side of it. Ravens, capuchins, marmosets, spider monkeys and all the great apes follow human gaze geometrically (Tomasello *et al.* 1999; Bugnyar *et al.* 2004; Bräuer *et al.* 2005; Burkart & Heschl 2006; Amici *et al.* 2009), and tamarins (Neiworth *et al.* 2002) and chimpanzees (Hare *et al.* 2000, 2001, see also Melis *et al.* 2006), though not capuchins (Hare *et al.* 2003), also of conspecifics in competitive situations. While empirical data for most animal groups are still needed (and particularly evidence that gaze following represents more than an orienting reflex), gaze following seems to be a taxonomically widespread characteristic of social species (Zuberbühler 2008).

1.3.6 Models of gaze following

Despite evidence that non-human species can follow the attention (and eye gaze) of others, there is considerable debate about what (if any) cognitive understanding they have of other's gaze and attention. Two models have been advanced to describe the cognitive mechanisms governing gaze following. The orienting response model, a cognitively low-level interpretation, holds that animals may process gaze and orientational information without reference to mental states, and have an innate reflexive and/or learned tendency to look in the direction of others' attention, that is reinforced over time by the usual presence of a visible target (Corkum & Moore 1998). A neurological basis for this is evidenced by cells in the parietal and temporal cortices of humans and monkeys that respond selectively to changes in gaze direction, and in humans, lesions in those areas impair gaze following (Emery 2000). Humans and macaques rapidly follow the direction of others' gaze in a way suggesting such a social reflex (Perrett *et al.* 1985, 1992; Friesen & Kingstone 1998; Driver *et al.* 1999; Langton & Bruce 1999; Deaner & Platt 2003; Hietanen & Leppänen 2003). Such reflexive gaze following, however, involves (and is possibly 'gated' by) non-reflexive components related to e.g., relative status. Although low-status rhesus macaques reflexively follow the gaze of all familiar conspecifics, high-status macaques tend to follow the gaze of only other high-status individuals (Shepherd *et al.* 2006). According to the orienting model, however, neither *direct* nor *geometric* gaze following provide evidence that animals conceptualize others in terms of underlying mental states (i.e., what they can and cannot *see*). Indeed, according to the orienting model geometric gaze following is possible, given a semi-reflexive gaze following ability coupled with experience of geometry, objects and obstructions (Povinelli *et al.* 2002; Gómez 2004).

The perspective taking model, a high-level interpretation, holds - as the orienting model - that gaze following is grounded in an orienting response, but also that individuals understand that others look because they see *something*. A high-level interpretation of geometric gaze following is therefore that individuals understand seeing as a psychological process, and attempt to take the visual perspective of others (Call *et al.* 1998; Okamoto-Barth *et al.* 2007a). Learning may influence both mechanisms. Individuals can *learn*, by means of classical conditioning, that the gaze direction of others is predictive of typical contingencies (e.g., the presence of an interesting event: the orienting response model), or may *develop* the understanding that others' visual perspective may differ from their own (the perspective taking model). An intermediate possibility is that prolonged gaze may be perceived to indicate a *connectedness* to something external (without ascribing the mental experience of *seeing* to another individual), which combined with knowledge of contextual and social contingencies, can help predict subsequent

behaviour. The question becomes whether non-human animals, as children, progress from a contentless automatic gaze following reflex to understand the mental experience and intentionally referential nature of gaze.

While it remains disputed whether non-human apes' gaze and point following reflect an understanding of others' mental states, there is considerable evidence that, in conjunction, suggests that apes do not simply respond automatically to others' gaze. First, apes follow human gaze geometrically by locomoting around obscuring barriers, and ignore an interesting distracting object (a novel toy), while tracking a human's gaze to an object behind themselves (Povinelli *et al.* 1996; Tomasello *et al.* 1999; Bräuer *et al.* 2005). Moreover, chimpanzees and bonobos (though not gorillas and orangutans) follow experimenter gaze more often when a clear barrier is placed in front of the experimenter's line of light, compared to an opaque barrier (Okamoto-Barth *et al.* 2007a). This suggests an understanding of the effect of barriers and a connection between the observed individual and an external target.

Second, like humans many primate species look back and forth between an experimenter's face and gaze direction when attention-following leads to no interesting sights, and track their gaze direction a second time (e.g., Scaife & Bruner 1975). Such gaze alternation (also termed 'double looks' and 'checking') is widely used to determine the understanding of the visual experience of others by preverbal children (e.g., Bates *et al.* 1975) and primates (great apes: Call *et al.* 1998; Bräuer *et al.* 2005; Diana monkeys: Scerif *et al.* 2004; macaques, *Macaca fascicularis*: Goossens *et al.* 2008; spider monkeys and capuchins: Amici *et al.* 2009), and has been interpreted as evidence that the gaze follower comprehends that gaze is referentially connected to something external, and expects the other to look at *something,* and that this expectation is violated by the absence of a visible target (the reason, for which the gaze follower performs a second 'checking' look). A lower-level interpretation of double-looks, however, is that animals, upon seeing nothing of interest, stop gaze following, and that the second look represents merely an independent, second automatic orienting response (e.g., Call *et al.* 1998). Nonetheless, this low-level interpretation of gaze alternation seems rather improbable in the light of examples of a high number of gaze alternations during gorilla play interactions. For example, Tanner and Byrne (2010) found that gorillas repeatedly (up to 8 times in succession) alternated gaze between a conspecific and a play object or external event, thus suggesting an understanding that gaze, and consequent behaviour, is referentially connected to something external.

Third, there is evidence of an ontogenetic progression of gaze following in chimpanzees (and macaques: Ferrari *et al.* 2000) comparable to that of children. Although there are temporal

differences in the onset of different 'levels' of gaze following in humans and chimpanzees, the development follows a similar trajectory. One chimpanzee with extensive experimental experience, reliably followed the head orientation of a human experimenter to targets within its own view by 11 months of age (compared to 9-10 months in children: Corkum & Moore 1995; Okamoto *et al.* 2002), of eye orientation alone by 13 months (compared to 14-18 months in children: Corkum & Moore 1998; Okamoto *et al.* 2002), and to locations behind itself by 20 months (compared to 12 months in children: Deák *et al.* 2000; Okamoto *et al.* 2004). Chimpanzees with less experimental 'training' follow human head and gaze orientation to targets outside their own visual field between 36-48 months (Tomasello *et al.* 2001). Unlike infant chimpanzees, adults observing a human continuously looking into empty space, habituate and stop responding (i.e., stop gaze following; Tomasello *et al.* 2001), suggesting that, in contrast to infants, adults can go beyond the orienting response when they find nothing of interest (Bräuer *et al.* 2005; Gómez 2005). With respect to using experimenter-given cues to select one of several baited containers in an object-choice task, longitudinal study of three chimpanzees demonstrated improvement with age and experience, and an increasing responsiveness to less salient cues. The chimpanzees used tapping and touching cues by approx. 12 months of age, and point cues before 24 months, with an understanding of the salient whole-hand point preceding the less salient index finger point, and proximal points (5 cm distance to object) preceding distal (20 cm) points (Okamoto-Barth *et al.* 2008). While the longitudinal nature of the particular study makes it difficult to disentangle the effects of learning from age, and allows for the possibility that subjects may simply have formed associations between increasingly sophisticated/subtle cues and events, the overall body of research suggests a developing flexibility of gaze following, and that adult chimpanzees understand that others may have a different visual perspective. Overall, these lines of evidence suggest that apes do not simply respond automatically to others' gaze.

1.3.7 The object-choice paradigm

While there is considerable evidence that many non-human primate species follow others 'gaze to locations behind barriers and themselves, this contrasts almost strikingly with the failure of the same species (and indeed, often the same individuals of those species) to use human gaze and other deictic gestures as cues to the location of hidden food. Non-human primates almost invariably fail tests based on the cooperative object-choice task (Itakura *et al.* 1999; Call *et al.* 2000; Povinelli *et al.* 2000; Hare & Tomasello 2004), which poses an evolutionary puzzle, as it raises the question as to the function of the animals' seemingly strong gaze following skills, if

these are not used to locate hidden objects and food. Recent work, however, suggests that while primates may find it difficult to use human gaze cues in the object-choice task, they readily, though at low levels, use conspecific gaze cues to 'prime' their responses and choices. Research has shown that lemurs successfully co-orient to the gaze direction of conspecifics shown in photographs, and use those gaze cues to selectively choose boxes, containing hidden food, located in the direction that the conspecific in the picture looks (Ruiz *et al.* 2009). While the lemurs showed relatively low (and non-significant) levels of (i) following the depicted conspecific's gaze and (ii) subsequently choosing the object, at which the conspecific gazed, the researchers suggested that this was a function of the overall low levels, at which the gaze of the individual in the static picture was followed. When the researchers examined the probability of choosing the object, at which depicted conspecific gazed in trials only, in which the subject had initially followed the conspecific's gaze, the success rate was high. The researchers consequently pointed out that many previous studies have not properly taken this into account (i.e., low overall rates of gaze following of a static model), and that when reanalysed, data from many primate species are likely to show correct object-choice as a result of gaze following. Thus, there is thus some suggestion (and potentially increasing) evidence that non-human primates can deploy conspecific gaze cues to locate hidden resources.

Moreover, perhaps importantly (although this was not tested in the lemur study and remains yet untested in general), animals may be more likely to deploy the gaze cues in an object-choice situation, when the cues are provided by a socially dominant individual of the animal's group, rather than a human experimenter. While the experiment did not examine the potential effect of social dominance (and thus cannot provide direct evidence to this effect), the lack of consideration of the relative social dominance relationships of the individuals used and tested in most other object-choice tests is puzzling.

While non-human primates' are generally unsuccessful at using cooperative human cues to locate hidden resources, certain methodological issues improve their performance on the object-choice task. Chimpanzees, for example, perform marginally better when experimenters precede a gaze direction cue by either a nonsense word, a chimpanzee bark or a food grunt (Itakura *et al.* 1999; Call *et al.* 2000; Lyn *et al.* 2010). The experimenters thereby precede their directional cues by a clear 'ostensive cue' (which may be defined as "showing that one wants to show something": Gómez 1996, p. 80). The animals' may perform marginally better in this context simply because the experimenter provides a clear indications that (s)he wishes to intentionally communicate with the subject (i.e., provides a far more conspicuous cue to this

effect, than that of simply capturing the subject's attention via mutual gaze and subsequently alternating gaze between the indicated object and the subject).

Primates, moreover, seem to find proximal pointing easier than distal pointing, and proximal cues (10 cm: Itakura & Tanaka 1998, Peignot & Anderson 1999) typically produce more correct responses than distal cues (e.g. 40 cm) (for a review, see Miklósi & Soproni 2006). One possibility is that highly proximal pointing gestures (e.g., 2-10 cm distance) may implicate 'low level' association learning processes (such as human-hand-food associations: Miklósi *et al.* 2003; Reid 2009) and provide a salient local enhancement cue. Local enhancement is defined as the drawing of attention to objects (or the location of objects) that others interact with (see e.g., Heyes 1994). Since non-social cues (such as movement) near or of objects capture the attention of humans (e.g., Itakura 2001), successful use of highly proximal pointing gestures by non-human primates may rest on 'simple' local enhancement, and thus deployment of, effectively, non-social cues, rather than reflecting an understanding of the referential and informative intent of the human experimenter.

Alternatively, a recent finding that apes perform better when experimenters make highly distal rather than comparatively more proximal points (100 cm vs. 40 cm distance) to one of two containers positioned far (250 cm) apart, has led to the suggestion that apes' typical poor performance rest on methodological rather than cognitive factors (Mulcahy & Call 2009). The authors observed that proximal pointing to one of two closely positioned containers entail that containers and experimenter cues "occupy the same visual plane, except that the containers occupy the foreground while the cues appear in the background" (Mulcahy & Call 2009, p. 307), The authors suggested that the typical association between the containers and food, and that the apes initially perceive only the containers, lead the prominence of the containers to override the apes ability to encode the experimenters cue. By contrast, distal points to widely spaced containers, lead the apes to initially perceive the cue, not the containers. Given the apes' poor performance in the proximal, but not distal condition, and since the proximal pointing condition in the experiment (40 cm distance) was within the range typically used for primates (e.g., 10 cm: Itakura &z Tanaka 1998), and of what has been operationalised as distal points in other experiments (e.g., 50 cm, Wolves, *Canis lupus lupus*: Miklósi *et al.* 2003; 60 cm), the suggestion goes some way to elucidate the apes' typical poor performance on the object-choice task.

Chimpanzees, surprisingly, perform perfectly when tested under a procedure where subjects enter the experimental scene anew on each trial, to see the experimenter gazing at the baited box (Barth *et al.* 2005). While Barth and colleagues suggest that the typical object-choice

test (in which subjects remain in the experimental area between trials) masks otherwise present abilities to exploit cooperative human cues, that the 'leave' version reveals, it is more parsimonious to assume that subjects in the 'leave' version simply used adventitious cues as to the experimenter's focus of attention, than comprehended the communicative intent of the gaze cue. Given the general primate ability to co-orient to the locus of others' attention, and the uncertainty of the situation (for subjects who do not comprehend the experimenter's collaborative, communicative intention), the logical choice is the box upon which the experimenter gazes, as gaze often signals interest. Insight into the communicative intention of the human pointer is therefore unnecessary, and skilful use of adventitious cues suffices. There is, however, some suggestion that gorillas (Peignot & Anderson 1999), one capuchin (Itakura & Anderson 1996), orangutans and chimpanzees (Itakura & Tanaka 1998; Byrnit 2004, 2009) can learn to use gaze cues, and improve after extensive training on the object-choice task. Indeed, both bonobos and chimpanzees, reared in socio-linguistically complex environments (where two-way communication with humans is promoted), select the correct container when experimenters produce a vocalisation, provide a proximal point (2-10 cm distance to the container), and alternate gaze between the subject and the correct container (Lyn *et al.* 2010).[10]

Apes' general poor performance on the object-choice task is puzzling, given evidence of some understanding of others' visual perception and intentions. Apes, for example, preferentially produce visual gestures when their recipient faces them (e.g., Liebal *et al.* 2004a,b), and chimpanzees understand that what others see influence their behaviour, and behave differently in competitive situations if a competitor sees a contested food source. They pursue contested food only if a conspecific competitor cannot see it (Hare *et al.* 2000; Hare *et al.* 2001) and conceal their approach when competing against a human experimenter (Hare *et al.* 2006; Melis *et al.* 2006). Furthermore, chimpanzees and orangutans show some understanding of the intentions underlying others' behaviour, and discriminate between the intentions of experimenters who accidentally or intentionally mark one of two boxes in an object-choice situation, or are unwilling or unable to give them food (Call & Tomasello 1998; Call *et al.* 2004). While chimpanzees fail to comprehend the human pointing gesture in cooperative food finding object-choice tasks, they are skilful at picking up adventitious referential information in competitive contexts. When an experimenter attempts to reach for a contested food source,

[10] One of six chimpanzees raised under standard conditions for captive apes (i.e., where regular human contact is limited to husbandry and cognitive tests have "no specific emphasis on understanding human communication": Lyn *et al.* 2010, p. 361) also passed the object-choice test. The authors, however, provide not supplementary information or explanation for the individual's performance.

chimpanzees successfully select the object the experimenter extends an arm towards, a gesture not unlike the cooperative pointing gesture (Hare & Tomasello 2004).

Much attention has been devoted to the possibility of homologous human-like joint attention abilities in the phylogenetically distinct canid group. While domestic dogs, *Canis lupus familiaris,* do not follow human gaze into empty space (Agnetta *et al.* 2000), they are skilled at using gaze and points to locate hidden food (Hare *et al.* 1998; Miklósi *et al.* 1998; Hare & Tomasello 1999; Soproni *et al.* 2001; Udell *et al.* 2008), preferentially beg from people who face towards them and have open eyes (Gácsi *et al.* 2004), discriminate human visual access to objects behind transparent and opaque barriers (Kaminski *et al.* 2009), and are less likely to approach forbidden food in the presence of an attentive human, than when the human is absent or looking away (Call *et al.* 2003). A lack of difference in the point following skills of kennel- and hand-reared puppies, and of puppies across a 2-14 month age span (Agnetta *et al.* 2000; Hare *et al.* 2002; Riedel *et al.* 2008), suggest that exposure to human interaction has limited effect on dogs' sensitivity to human communicative cues, and that this adaptation emerges spontaneously, at a young age. In contrast to domesticated species such as dogs, cats, *Felis catus* (Miklósi *et al.* 2005), goats (Kaminski *et al.* 2005), horses, *Equus caballus* (Maros *et al.* 2008)[11], and of captive foxes, *Vulpes vulpes,* selectively bred for fearlessness and non-aggression towards humans (Hare *et al.* 2005), some studies suggest that neither wolves raised in zoological settings (Agnetta *et al.* 2000), nor those with considerable human experience (Hare *et al.* 2002; Virányi *et al.* 2008), respond to human pointing gestures. This has led to the 'social domestication hypothesis', which holds that domestication (rather than human exposure during ontogeny) has played a dominant role in shaping dogs' sensitivity to human communicative cues (Hare *et al.* 2002). Through domestication dogs not only reduced their fear of humans, but also, over evolutionary time, applied and adapted general problem-solving skills to social interactions with humans (Hare & Tomasello 2005; Hare 2007). According to an extension of this proposal, dogs have thereby acquired insight into the *intention* of human pointers, and thus possess an aspect or precursor of a ToM (Miklósi *et al.* 2000, 2004). By extension, the hypothesis applies to non-human primates who, by virtue of lack of domestication, are predicted to respond weakly to human cooperative, communicative cues.

[11] McKinley & Sambrook (2000) found that one of four horses used distal points to chose one of two buckets, and Marsos and colleagues (Marsos *et al.* 2008) that a group of 20 horses made use of momentary proximal, and sustained proximal and distal points (although not momentary distal points). Horses were, however, held on a lead-rein and encouraged by owners, leading to the suggestion that the 'Clever Hans effect' may have been implicated (Reid 2009).

Recently, however, the strength of empirical evidence supporting the social domestication hypothesis has been questioned on methodological and analytical grounds, and by contrasting data (see e.g., Wynne *et al.* 2008; Hare *et al.* 2010; Udell & Wynne 2010). While wolves perform poorly when tested under different experimental setups than dogs (i.e., with humans positioned outside their enclosures, requiring the wolves to move through multiple cages to get the reward, a condition found to limit the performance in dogs: Udell *et al.* 2008), hand-reared wolves tested under conditions comparable to dogs (with no fence separating subjects and experimenters), respond to human pointing at levels comparable (Gácsi *et al.* 2009a) and superior to dogs (Udell *et al.* 2008). Moreover, recent study (and personal observation) suggest that ontogeny *does* contribute to dogs' understanding of human communicative cues (Gácsi *et al.* 2009b; Costa *et al.* 2010), and that the failure of previous studies to demonstrate an effect of human interaction, owes to a methodological flaw of comparing subject groups with similar degrees of human experience and interaction (family- and kennel-reared dogs). As an alternative, van Rooijen (2010) suggests that responsiveness to human pointing cues separates along a species line of, not domestication, but cooperative foraging. Cooperatively foraging species include wolves, lions and dogs, though not chimpanzees who, despite hunting in groups, show little evidence of hunting *cooperatively* (for a cooperative interpretation of hunting by Taï chimpanzees, see e.g., Boesch 1994, 2002).[12] Van

[12] According to the traditional definition cooperative behaviour (a behaviour whose outcome increases fitness of the participants: Hamilton 1964) chimpanzees a Taï National Park (Boesch & Boesch 1989, but no Gombe National Park: Busse 1978) hunt cooperatively. That is, hunting success increases with group size, and is larger for multi-male than single-male groups. While chimpanzees forage in groups and cooperate in a broad sense, there is little experimental and unequivocal observational evidence that they engage in collaboration (and by implication, true collaborative hunting), in the narrow sense, i.e., engage in interactions involving joint goals and intentions, and attend to things jointly, based on coordinated plans (Tomasello *et al.* 2005). For example, while Boesch argues that chimpanzee hunters perform complementary roles that may shift during hunts, thereby "demonstrating a capacity for role reversal and perspective-taking" (Boesch 2005, p. 692), such observations are plausibly explained with reference to lower-level cognitive processes, whereby the apes are responsive to others *behaviourally*, and individually assess the state of the hunt on a moment-to-moment basis (Tomasello *et al.* 2005). Indeed, controlled studies of captive, non-language trained chimpanzees, suggest that they perform poorly in role-reversal tasks, where individuals play different and complementary roles (for a role-reversal study see Povinelli *et al.* 1992, but also Tomasello & Call 1997 for an interpretation not involving understanding of role reversal). [In contrast, the two chimpanzees, Sherman and Austin, who had received extensive teaching in symbolic communication, nevertheless appeared to perform well on role reversal tasks: Savage-Rumbaugh 1986]. Moreover, while chimpanzees perform well in food-finding object-choice tasks structured around competition, they typically fail the cooperative version (e.g., Hare & Tomasello 2004); they show limited communication about third entities, and no 'showing' signals with an (unambiguous) declarative or informative motive. Furthermore, an observational study of captive chimpanzees revealed no inter-animal negotiation in general, and no negotiation over the intended meaning of signals, or requests for

Rooijen's suggestion is, however, problematic, as there is there seems to be no directly comparable data to demonstrate that the cooperative hunting of wolves and dogs differ from that of chimpanzees in terms of underlying cognitive processes, such as shared intentionality.

Demonstrations that both bonobos and chimpanzees, reared in socio-linguistically complex environments, pass an object-choice task involving highly proximal pointing (2-10 cm), suggest that either such proximal pointing produces an effective (essentially, non-social) local enhancement cue, or it lies within the capacity of at least two species of non-human great apes to deploy intentionally, purely informative, human social cues when the individuals have received particular rearing experiences (Lyn *et al.* 2010). While the social domestication hypothesis provides a nice framework, its explanatory strength, as applied to non-human primates, is somewhat questionable. Further research is required to elucidate the underlying differences within and between species passing object-choice tasks, and to disentangle the effects of domestication and 'enculturation' (and any potential interactive effect), and if, for example, enculturation overrides domestication effects, or if domestication simply has less explanatory value than originally granted.

1.4. Triadic interactions, soliciting of interaction, help and information

1.4.1 Referential looking and social referencing

Referential looking has been defined as looks to another individual that are immediately preceded and/or followed (within 2s) by a look to an object (Russell *et al.* 1997; Roberts *et al.* 2008), and some have suggested that the definition provides a means to determine if an individual looks to another to seek information, or for other purposes, such as reassurance (Clyman *et al.* 1986, cited by e.g., Roberts *et al.* 2008). Indeed, in both human-reared chimpanzees and Barbary macaques (*Macaca sylvanus*) older infants produce more frequent

clarification (Liebal *et al.* 2004b). While there is persuasive evidence that chimpanzees (Leavens *et al.* 2005) and orangutans (Cartmill & Byrne 2007) attempt to repair failed communication with humans who fail to give requested food items, Tomasello (1998) has argued that non-human primates' signals lack the bidirectionality of human signals, whereby senders and receivers are aware that they can play both 'roles', and that apes "do not know it is the same signal when they send as when they receive it" (Tomasello *et al.* 2005, p. 685). These differences in definitions regarding what constitutes cooperation have led to different interpretations as to whether chimpanzees do (e.g., Boesch 2005) or do not (e.g., Tomasello *et al.* 2005; van Rooijen 2010) engage in actual cooperative hunting.

referential looks to caregivers in situations of uncertainty, than younger infants do (Russell *et al.* 1997; Roberts *et al.* 2008), which lends *implicit* support to this suggestion (i.e., a larger proportion of referential looks by *younger* infants in situations of uncertainty, would support a 'reassurance-interpretation' of 'referential looks').

Social referencing is defined as the active seeking and subsequent use of emotional information from others to evaluate ambiguous objects or events (Klinnert *et al.* 1986, cited by Russell *et al.* 1997). The simple triadic triangle encompasses (i) a subject, (ii) a referent (an ambiguous object or event), and (iii) an individual whose emotional state is sought and used, and includes (i) referential looks between the object/event and other individual, and (ii) behavioural regulation on the basis on the emotional information received. Such reading and use of others' emotional responses is highly adaptive, as it allows naïve individuals to learn the meaning of novel objects and situations, without engaging in potentially costly trial-and-error learning.

In normally developing human infants, social referencing emerges towards the end of the first year, when infants begin to coordinate looks between people and objects. This ability of infants to guide their behaviour on the basis of the emotional cues of others, has by some (e.g., Baron-Cohen 1995) been considered a simple behavioural manifestation of the understanding that others have intentions and emotions that may be directed towards external things, and consequently viewed as a basic precursor for later emerging theories of mind. Traditional social referencing paradigms involve exposing subjects to ambiguous situations, strangers or novel objects, and let caregivers provide different emotional messages. While two experimental studies of captive mother-infant chimpanzee pairs found little evidence of infant social referencing (Itakura 1995; Tomonaga *et al.* 2004), human-reared chimpanzees exposed to a novel toy look referentially to their human caregivers and adjust their behaviour according to the valence of the message they receive (Russell *et al.* 1997). The significance of the potential effect of human enculturation on social referential engagement, however, remains poorly understood.

1.4.2 Triadic interaction, and soliciting of help and objects

Controversy remains regarding apes' ability to share attention in a coordinated, triadic manner. For example, human-raised chimpanzees do not coordinate attention with humans in neither role-reversal nor object-choice tasks (Tomasello & Carpenter 2005), and a comparison of children, and human- and mother-reared chimpanzees and bonobos suggest that children spend far more time engaged in joint attention behaviours (e.g., gaze following, pointing, and

gaze alternation) than non-human apes, with human-raised apes falling in between children and mother-reared apes (Carpenter *et al.* 1998).

Moreover, while chimpanzee infants engage in mutual gaze with their mothers, and follow human gaze, there is little evidence that they actively coordinate attention between objects and humans (Okamoto-Barth & Tomonaga 2006) or conspecifics (Bard & Vauclair 1984). Indeed, chimpanzee and bonobo mothers rarely manipulate objects in the presence of their offspring, and when observed to do so, infants do not coordinate attention between the objects and their mothers (Bard & Vauclair 1984). Recent research, however, suggests that juvenile and adult individuals of all the great ape species alternate gaze between humans (and conspecifics) and an object held by the human (Pitman & Shumaker 2009). Moreover, chimpanzees engage in gaze alternation during imperative food and object requests (Leavens & Hopkins 1998), and gorillas when requesting that a human perform an action for them (e.g., Gómez 1996). The actual meaning of these stimulus-other-stimulus gaze shifts, however, remains debated.

Joint attention (versus joint attention *behaviours*) is widely defined as involving the mutual awareness that two or more individuals attend to a common focus (e.g., Tomasello 1995; Leavens & Racine 2009). While Tomasello initially suggested that gaze alternation implies such awareness, such a rich interpretation of gaze alternation has been questioned on the basis of e.g., the nature of gaze alternation of non-human primates. For instance, human infants engage in longer (almost twice as long) and more frequent episodes of gaze alternation than chimpanzees (Carpenter *et al.* 1995), and while human joint attention episodes are often accompanied by infant smiling (interpreted as implying a desire to share an experience), lack of smiling during non-human joint attention episodes has given rise to the (rather surprising and tenuous) suggestion that apes look to others to simply monitor and predict their subsequent actions ('checking looks': Tomasello & Carpenter 2005), rather than to e.g., share a mental experience ('sharing looks': ibid.).

The seeking of emotional information and behavioural adjustment according to the valence of the message received by chimpanzees during tests of social referencing (Russell *et al.* 1997), however, suggest that apes' looks to others may be based on more than mere 'surface' predictions of others' behaviour, and that the apes may understand some of the underlying elements involved in some form of basic, coordinated attention (for example, that emotions can be directed at external things).

Since much ape social interaction around objects in has been suggested to be competitive, some of the most successful studies of possible coordinated attention in apes have

examined contexts, in which competition is limited and cooperation already manifest. That is, in play contexts and mother-offspring interactions. In these contexts, apes may sometime actively solicit aid and other forms of interaction from others. For example, Plooij (1978) described examples of a chimpanzee (in the wild) picking up an object, and beginning to run away from another individual, while looking back at the individual, which might then give chase. Moreover, in the context of playing social games, bonobos sometimes re-engaged a suddenly passive human partner by means of e.g., head bobbing, stomping, and grabbing and touching the human's hand (Pika & Zuberbühler 2008), suggesting that the bonobos were aware of the joint activity and actively tried to re-engage the human therein. Furthermore, Tanner & Byrne (2010) reported a number of cases, in which juvenile and adult gorillas engaged in joint attention, and collaborative and triadic interactions during play with conspecifics. The gorillas frequently engaged in repeated bouts of gaze alternation between a play object and a social partner. While gaze alternation does not represent an unequivocal sign of joint attention (as it may simply function to check the interest, proximity and movement of others), the gorillas engaged in repeated bouts of gaze alternation to the same social partner, suggesting that they were actively sharing an experience (i.e., the game). Moreover, the authors report a number of cases in which objects were intentionally held up, shaken and shown to the conspecific.

Gorillas will sometimes take a human's hand, and lead a person to a door to be opened, while exchanging looks between the door and human (Gómez *et al.* 1993), and in a task requiring cooperation by two individuals to retrieve food, chimpanzees readily solicited help from a human partner, by whimpering, taking the hand and looking at the face of the human partner (Hirata & Fuwa 2007). While the chimpanzees did not spontaneously solicit help from conspecifics in a similar cooperative task (Hirata & Fuwa 2007), they may learn to do so. In a classic study of cooperation (upon which the aforementioned cooperation task was based), Crawford (1937, cited by Hirata & Fuwa 2007) reported that some chimpanzees eventually, actively, began to encourage conspecifics to cooperate, by means of gaze, gestures and physical contact. Finally, a recent study has shown that, when placed in two adjoining cages, where one chimpanzee had access to an out-of-reach food item, and its nearby conspecific was supplied with a tool to retrieve the food, individuals spontaneously requested the tool (by means of e.g., whole-hand reaching/gesturing), and the tool was subsequently delivered by the conspecific (Yamamoto *et al.* 2009). The complex experimental history of the chimpanzees (who had participated in numerous cognitive studies, including tasks involving reciprocity, and food- and token-sharing), however, raises the possibility that the behaviour may reflect cooperative capacities and expectations that do not necessarily extend to interactions between less 'trained' individuals.

The 'Enculturation Hypothesis' (Call & Tomasello 1996) posits that rearing and engagement in a human socio-cultural environment allows great apes to acquire cognitive abilities more typical of human cognition than that of their own species. Undeniably, some of the apes that engaged in the instances of triadic interaction reported above had received much such human interaction during ontogeny (e.g., Gómez *et al.* 1993; Hirata & Fuwa 2007; Yamamoto *et al.* 2009). Others, however, interacting with conspecifics, did not have such similar histories (see Pooij 1978; Tanner & Byrne 2010), and extensive human influence during ontogeny (and an 'updating' of their abilities to somewhat match those of human infants), does therefore not seem to have been the case. Non-human apes will, thus, under some circumstances, solicit aid and interaction from others. Still, controversy remains regarding apes' sharing of attention in a coordinated, triadic manner, as does the argument that particular joint attention behaviours are qualitatively different in humans and non-human apes (e.g., Tomasello & Carpenter 2005). Since joint attention is most convincingly demonstrated if one individual spontaneously initiates re-direction of another's attention, the next section examines the occurrence of this in non-human primates and human development and communication.

1.5 Pointing without deixis

1.5.1 Identifying communicative gestures

A pivotal issue in the study of primate communication is the understanding that individuals have of the communicative signals they and others produce. A subset of communicative acts suggests that individuals make informed choices about the effects of the their communicative signals. These entail that signallers intentionally adjust their communicative gestures for the purpose of influencing others. Given, however, the intricacy of establishing intentionality in non-linguistic communication, distinctions are typically made on the basis of the following criteria: (i) establishing mutual gaze to control recipient visual attention, (ii) gaze alternation, (iii) flexibility of communicative means (i.e., that individuals may use different means towards the same end, and the same means towards different ends), (iv) goal orientation, (v) response-waiting (waiting after the signal has been produced, expecting a response), and most importantly, (vi) that signals are used socially and adjusted to the attentional state of the audience (e.g., Piaget 1952; Bates 1976; Bruner 1981, cited by Pika *et al.* 2007; Gómez 1991; Bard 1992; Tomasello *et al.* 1994; Leavens & Hopkins 1998; Hosetter *et al.* 2001). These criteria help distinguish intentional gestures as an important and flexible subset of communicative behaviours, compared to many more stereotypic gestures

1.5.2 Definitions of pointing

In human daily interaction, the canonical pointing gesture is ubiquitous and serves as a foundational building block for declaring, referring, asking and making a point. While head pose is an adventitious and often unintended consequence of visual attention, pointing provides a more explicit directional cue and is usually intended for attention direction (Deák & Triesch 2006). Pointing is considered an important component of joint attention, and has, by virtue of its triadic referential function (by including a signaller, a recipient and establishing a connection to a third entity or event), been cast as a behavioural stepping-stone for labelling, symbolic reference and language development (e.g., Bates *et al.* 1975; Butterworth 1998; Goldin-Meadow & Butcher 2003).

Bates, Camioni and Volterra (1975) suggested a distinction between proto-imperative and proto-declarative pointing (henceforth imperative and declarative), and that while imperative pointing involves using another individual as a means to an end (obtain objects, be picked up etc.), the object pointed to in declarative communication is the *means*, and the actual *interaction* with the other individual the *end* ("laughter, comment, smiles and eye contact – which we have termed attention": Bates *et al.* 1975, p. 216). Crucially, Bates and colleagues explicitly defined both gesture types as instrumental acts, i.e., both were defined as a subset of imperative signals, used to provoke some form of behavioural response. Since then, imperatives and declaratives have received different interpretations, with the majority of formulations (though by no means all, see e.g., Gómez *et al.* 1993; Racine *et al.* 2008) suggesting that they reflect a considerable difference in the underlying psychological processes. Some argue that the main difference between the gestures lies in representational ability (Baron-Cohen 1991; Tomasello 1995; Camaioni *et al.* 2004), others in motivation (e.g., Gómez *et al.* 1993). The 'representational difference' view has given imperative gestures a behaviourist interpretation ('*give* me that') and declarative gestures a mentalistic interpretation ('*look* at that'). Accordingly, imperative gestures are held to reveal a causal understanding of others' physical agency and may be a simple physical interaction, in which the sender acts to change the recipient's behaviour (rather than state of mind), and may be learned by virtue of contingencies. Since both autistic children and many primates use imperative (and not declarative) signals, the 'representational difference' view has cast imperatives as fairly trivial. In contrast, declarative gestures have been interpreted as revealing sensitivity to others' mental agency and a desire to share attention, experiences and interest, thus implying an ability to represent others' mental states. Declarative gestures have thus been cast as a precursor to a ToM (e.g., Baron-Cohen 1991) a behavioural stepping-stone for symbolic reference (Bates *et al.* 1975; Butterworth 1998), the development (e.g., Butterworth

2003) and evolution of language (Hewes 1981), and a species-specific human trait (Eibl-Eibesfeldt 1989; Donald 1991; Povinelli & Davis 1994), reflecting an evolutionary and ontogenetic entry into a world of shared intentionality (Tomasello & Carpenter 2007), and an evolutionary discontinuity in the understanding of meaning as communicated in an inter-subjectively shared world (Brinck & Gärdenfors 2003; Tomasello 2006).

This classical view of imperative and declarative pointing has, however, created a seemingly false dichotomy, that understates any possible consideration of others' attentional and mental states involved in imperative pointing, and overstates the pro-social and cooperative motive underlying declarative pointing (Gómez *et al.* 1993; Southgate *et al.* 2007). Alternatively, the 'motivational difference' view holds that imperative and declarative gestures do not differ at the level of required representation, but in motivation. Accordingly, declarative gestures need not involve an understanding of others' mental agency, and can be used simply to elicit an emotional and/or attentional reaction in others (Gómez *et al.* 1993). Both emotional and attentional states are reflected in overt facial expressions and behaviours, and the desire to provoke them in others does therefore not require an ability to represent mental states, and a wish to elicit a mental experience. All it requires are *in*tentional states about others' *a*ttentional states (as reflected in overt behaviours), and an understanding of a link between the overt manifestations of attentional and emotional states of others. According to this view, individuals may point declaratively, to monitor the addressee's attentional and emotional responses to objects or events (Gómez *et al.* 1993), and the difference between the two gesture types therefore lies in making others react *behaviourally* (imperative) versus *look to* and *react emotionally* (declarative). Imperative and declarative pointing are thus viewed as equally good ToM precursors and their cognitive equivalence supported by their temporal co-emergence in children around 12 months (e.g., Carpenter *et al.* 1998). Although one study suggested that imperatives and declaratives emerge in sequence, with declaratives appearing later and being related to the emergence of intentional understanding (Camaioni *et al.* 2004), the study contained a significant methodological flaw[13], and all other studies have indicated a simultaneous emergence of the two types of pointing.

[13] While the study's imperative condition required 9-17 month olds to point to proximal targets (1m distance), the declarative condition required pointing to distal objects (3m). As there is some suggestion that proximal pointing emerges earlier in human development (and is more frequent) than distal pointing (e.g., Lock *et al.* 1990), the study confounded proximity and point type.

The different interpretations produce different and, in some cases, contradictory notions about the cognitive capacities required for declarative communication. For clarity, the main suggested motivations for pointing are listed below:

1. Pointing for imperative purposes: Pointing to request an out-of-reach object, or spur another on to perform some action on an object (Bates *et al.* 1975; Gómez 2004).
2. Pointing for informative purposes: Pointing to change others' knowledge about e.g., the location of an object, i.e., to "helpfully provide information for the other" (Liszkowski 2005, p 147).
3. Pointing for declarative purposes:
    a. Pointing to show, but not possess an object (Bates *et al.* 1975); Pointing to obtain an *interaction* with the other individual ("laughter, comment, smiles and eye contact – which we have termed 'attention": Bates *et al.* 1975, p. 216).
    b. Pointing to elicit *interactions* and *appealing* behaviour from and with social partners (Moore & Corkum 1994).
    c. Pointing to *share* attention, attitudes (Liszkowski *et al.* 2004), emotions and experiences with the addressee (Tomasello 1999); Pointing to influence the mind of a social partner (Baron-Cohen 1989, 1995)
4. Pointing for social referencing purposes: Pointing to provoke an attentional response that can be used to monitor the addressee's attentional and emotional responses, and thereby discern ambiguity in situations of uncertainty, and provide information about an object or event, and how to respond (see e.g., Gómez *et al.* 1993). While this type of pointing has thus far been assigned a declarative label, it seems reasonable to treat it as an independent category. Social referential pointing neither functions to '*share'* attention, attitudes or emotions, nor to elicit an 'interaction' as such, but simply to provoke an attentional/ emotional response, that the subject can deploy for social referencing purposes.

Thus, while imperative pointing, minimally, involves a behavioural-based understanding that attentional states can produce behaviours that can be used to attain object-related goals, declarative and informative pointing is taken to entail some understanding of the interlocutor's perceptual and informational states (Liszkowski *et al.* 2007). By contrast, social referential pointing, minimally, suggests that one conceives others as having emotional and/or behavioural responses towards the environment, that may be elicited by manipulating their attention (without necessarily representing the mental implication thereof).

The behavioural criteria that distinguish the different forms of pointing rest on whether the 'pointer' seems 'satisfied' with the reaction of the other individual, and indeed modifies his or her behaviour as a function of the other's response to the pointing. An imperative motive in human infant pointing is typically inferred if the subject stops pointing if the other individual performs some form of action on the indicated object (e.g., gives the object to the subject). In contrast, the criteria for establishing a declarative motive is typically based on whether the subject is satisfied (i.e., ceases pointing), if the other individual simply looks to the indicated location and subsequently emotes positively to the infant (i.e., engages in an *interaction* with the subject *about* the indicated object).

Since social referential pointing is not about eliciting an *interaction* with the other, so as to *share* e.g., *attitudes* and *experiences*, but simply to provoke an attentional/emotional response, that the subject can use for social referencing purposes, pointing can be said to fall into this category if the subject adjusts its behaviour according to the valence of the other's emotional response the indicated object. For example, a fearful response in the other is predicted to evoke similar fearful behaviours in the subject, while approach and inspection of the object is predicted to make the subject more likely to do the same.

1.5.3 Non-verbal deixis in human development

Human infants show an extraordinary ability to follow the attention of their social partners, and, later in ontogeny, to intentionally secure and redirect the attention of others. The propensity to flexibly read and use pointing cues in communicative contexts develops around 9-12 months, before children acquire language (Tomasello & Rakoczy 2003), but around the time when they begin to use single-word utterances (e.g., Butterworth 2003). There is some disagreement about the relative timing of the emergence of point and head/gaze cue understanding. While many studies suggest that infants to *respond* to head and gaze changes prior to manual pointing (e.g., Butterworth & Jarrett 1991; Butterworth & Itakura 2000), others studies suggest that points and gaze are *understood* simultaneously towards the end of the first year (e.g., Corkum & Moore 1995), reflecting the emergence of an understanding of the referential nature of multiple cues. More recent studies suggest that understanding of pointing slightly precedes understanding gaze cues (Triesch *et al.* 2006), and when added to a gaze and head cue, increases attention following (Flom *et al.* 2004), and results in more accurate peripheral target localisation (Butterworth & Itakura 2000), possibly due to the higher

discriminative validity and salience provided by the motion of manual points (Deák & Triesch 2006).

Comprehension of pointing occurs towards the end of the first year, slightly in advance of production of the gesture. In typical human development, infants follow pointing to near objects around 9 months of age, and more distant objects around 12 months (e.g., Butterworth & Jarrett 1991). Although infants as young as 18 days have been observed to spontaneously extend the index finger from a closed fist (Hannan & Fogel 1987, cited by Kita 2003), these are undirected motor acts, not communicative acts. Longitudinal and cross-sectional studies show that infants begin to produce the canonical pointing gesture at an average of 11 and 12 months, respectively (longitudinal: Butterworth and Morissette 1996; Carpenter *et al.* 1998; cross-sectional: Leung and Rheingold 1981), although infants as young as 8.5 months have been observed to point communicatively (Butterworth & Morisette 1996). The pointing gesture emerges suddenly, as if after a stage transition (Butterworth 2003), and constitutes more than 60% of all infant gestures by 12 months (Lock *et al.* 1990).

1.5.4 Non-verbal deixis in non-human apes

Primates who are reared with human contact and have been explicitly (through teaching), or implicitly exposed to the functional aspects of human pointing, are able to attract and redirect others to things that they want (e.g., chimpanzees: Gardner & Gardner 1985; Woodruff & Premack 1979; Leavens *et al.* 1996, 2005; Krause & Fouts 1997; Leavens & Hopkins 1998; gorillas: Patterson 1978 cited by Racine *et al.* 2008; Gómez *et al.* 1993; orangutans: Miles 1990; Call & Tomasello 1994; macaques: Hess *et al.* 1993; Kumashiro *et al.* 2002; squirrel monkeys: Anderson *et al.* 2001). While however, there are numerous reports of apes spontaneously engaging in pointing to request objects, monkeys have only been reported to engage in pointing following explicit training, suggesting that the behaviour may come more easily to apes than monkeys.

Given the typically confined environment of captive primates, it is not surprising that they learn to use humans as an effective social tool to obtain out-of-reach objects ('social tool use': e.g., Bard 1990, Leavens e*t al.* 1996, 2005, 2008). The traditional low-level interpretation of non-human pointing holds that animals learn to point to desired objects outside the confines of their cages by means of blind trial-and-error learning. Captive chimpanzees, however, frequently combine multiple communicative signals (e.g., manual pointing gestures and repeated head/gaze

shifts) when requesting objects from humans, and take into account the attentional states of experimenters (e.g., Leavens *et al.* 2004) suggesting some understanding of others' attention and visual perspective.

It has been widely argued that apes do not point amongst themselves (e.g., Povinelli 2003; Moll & Tomasello 2007[14]). Nonetheless, there are numerous examples of apes in both captivity and the wild using manual pointing gestures and other forms of referential behaviours during communication with conspecifics. While observations from wild populations are, exceptionally rare (captive populations: Savage-Rumbaugh *et al.* 1977; de Waal 1982[15]; Bard & Vauclair 1984: Savage-Rumbaugh 1986[16]; Tanner & Byrne 1996; Tanner *et al.* 2006; Zimmermann *et al.* 2009; wild populations: bonobos: Veà-Sabater-Pi 1998; chimpanzees: Pika & Mitani 2006), recent study has shown that chimpanzees in the wild consistently, indicate parts of their own bodies that they seemingly want others to groom, by means of exaggerated scratching behaviours (Pika & Mitani 2006), suggesting that non-verbal deixis may be a more frequent component of the natural communication of wild ape populations than previously assumed. All of these gestures, however, are imperative and about spurring others into action to do something for the subject.

Zimmermann and colleagues (Zimmermann *et al.* 2009) found that bonobos and orangutans guided a human experimenter to the location of a hidden tool that was needed to retrieve food for the animals. The tool was hidden in the presence of the animal, but in the absence of the human experimenter. While bonobos and orangutans who participated in the experiment had extensive experience with the request and delivery of food and other items from and by humans (for details, see Appendix 3), the experiment demonstrated an ability to adjust communication in accordance to the human's knowledge/ignorance of the tool's location, and point to the location when needed. The proximate mechanisms and cognitive sophistication

[14] "there has not been a single reliable documentation of any scientist in any part of the world of one ape pointing for another"(Moll & Tomasello 2007, p. 643).

[15] E.g., de Waal reported the following interaction: "On a hot day two mothers, Jimmie and Tepel, are sitting in the shadow of an oak tree while their two children play in the sand at their feet. Between the two mothers the oldest female, Mama, lies asleep. Suddenly the children start screaming, hitting, and pulling each other's hair. Jimmie admonishes them with a soft, threatening grunt, and Tepel anxiously shifts her position. The children go on quarrelling, and eventually Tepel wakes Mama by poking her in the ribs several times. As Mama gets up Tepel points to the two quarrelling children. As soon as Mama takes one threatening step forward, waves her arm in the air, and barks loudly the children stop quarrelling. Mama then lies down again and continues her siesta." (de Waal 1982, p. 34).

[16] Savage-Rumbaugh (1986) observed one chimpanzee request food from another on repeated occasions during a cooperative laboratory task.

underlying this pointing behaviour remain obscure, and it is unclear if the pointing was motivated by an intention to inform the human experimenter about the tool's location (informative pointing: Liszkowski 2005), or a complex imperative request that the human recover and use to tool to retrieve food (Gómez 2004; Tomasello *et al.* 2007; Zimmermann *et al.* 2009). Overall, however, the capacity of apes to request absent objects (such as food or tools) does not require an informative explanation (Gómez 2007).

Declarative gestures have only been reported for human-raised and language-trained apes (Patterson 1978; Savage-Rumbaugh *et al.* 1986, 1998) and one wild bonobo extending an outstretched arm towards some poorly hidden nearby scientists and alternating gaze between the humans and its conspecifics (Veà & Sabater-Pi 1998)[17]. Importantly, these reports are anecdotal; in all cases interpretation is at issue, and the declarative intention may exist only in the eyes of the human beholder. Moreover, experimental measures that reliably educe declarative behaviours from human infants, have failed to do so from chimpanzees interacting with humans (Tomasello & Carpenter 2005). The conclusion typically drawn is that while non-human apes gesture imperatively, they do not share the human ability and/or motivation to communicate declaratively (e.g., Gómez *et al.* 1993; Povinelli & O'Neill 2000; Tomasello & Carpenter 2005). Despite an understanding of others' goals and intentions, it is widely argued that apes do not understand *communicative intentions*, do not know what is informationally new for others, and/or lack a motivation to share experiences, goals and intentions with others, and to help them by informing them about objects and events (Tomasello 2006).

A key component of intentionally referential behaviour is the ostensive component, ("showing that one wants to show something" Gómez 1996, p. 80). There is some evidence that human-reared gorillas engage in eye contact to control the attention of human experimenters, and follow such by requestive behaviours (Gómez *et al.* 1993), and that chimpanzees use mutual gaze to signal ostension before encouraging conspecifics to follow them to the location of hidden objects (Menzel 1973, 1974; Menzel & Halperin 1975). Moreover, eye contact and gaze

[17] "February 24, 1989. 13:09 h. Noises are heard coming from the vegetation. A young male swings from a branch and leaps into a tree […]. He emits sharp calls, which are answered by other individuals who are not visible. He points - with his right arm stretched out and his hand half closed except for his index and ring fingers - to the position of the two groups of camouflaged observers who are in the undergrowth (30 m apart). At the same time he screams and turns his head to where the other members of the group are. 13:12 h. The same individual repeats the pointing and calling sequence twice. Other neighbouring members of the group approach. They look towards the observers. The young male joins them." (Vea & Sabater-Pi 1999, p. 289).

alternation combined with imperative gestures have provisionally (though never officially[18]) been reported for bonobos presented with a human or conspecific holding a novel object (O'Connell 1994). De Waal (2001)[19] has consequently suggested that bonobos may use gaze as an intentional referential signal, in lieu of imperative manual pointing, by engaging in ostensive behaviour (i.e., establish attentional contact to signal communicative intent), and subsequently alternate gaze between the interlocutor and a desired object.

There are, a few series of studies that suggests that apes do produce spontaneous, complex referential behaviours to elicit an attentional reaction in conspecifics. For example, gorillas have been observed to repeatedly use apparent deictic manual gestures to seemingly draw conspecifics' attention to distal locations (Tanner & Byrne 1996)[20]. Moreover, Menzel and colleagues (Menzel 1973, 1974; Menzel & Halperin 1975) reported that when a lone chimpanzee was shown where food, or a frightening object, was hidden in an outdoor enclosure, the rest of its group grasped the valence and approximate location of the object when let into the enclosure. While most chimpanzees were led to the location by the adventitious, referential information that the informed chimpanzee emitted, some informed chimpanzees seemingly actively directed conspecifics to the appropriate locations by walking towards the spots, looking back at the others, waiting until they began to follow, and if not, pulling their arm or body and leading them towards the objects. Neither Menzel's nor de Waal's suggestions have, however, been "substantiated as more than personal impressions" (Tomasello 2006, p. 521).

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[18] O'Connell (1994, cited by Gómez 1996) reported the occurrence eye contact, gaze alternation and imperative gestures in bonobos presented with either a conspecific or a human holding a novel object, and argued that bonobos use gaze to regulate interactions with conspecifics. O'Connell also reported that bonobos frequently use gaze to regulate every-day (non-experimental) dyadic play interactions with conspecifics. The observations were reported at a conference, though never published. A number of flaws relating to the research program (R.I.M. Dunbar, *personal communication*) may account for the lack of publication, and suggests that the observations be treated with caution.

[19] Nikkie had gotten used to my throwing wild berries to him across the moat at the zoo where I worked. One day, while I was recording data about the apes, I totally forgot about the berries, which hung on a row of tall bushes behind me. Nikkie hadn't forgotten. He sat down right in front of me, locked his red-brown eyes into mine, and -- once he had my attention -- abruptly jerked his head and eyes away from mine to fixate with equal intensity on a point over my left shoulder. He then looked back at me and repeated the move. I may be dense compared with a chimpanzee, but the second time I turned to see what he was looking at, and spotted the berries" (de Waal 2001, p. B7). "Show us the cases where apes point things out to one another, the skeptics say. Unfortunately, they mean manual pointing, not Nikkie's pointing with his eyes, or the whole-body point noted by Menzel -- methods that are far more common." (de Waal 2001) p. B8).

[20] E.g., Kubie a male gorilla at San Francisco Zoo, occasionally produced "[a manual knocking gesture that] in some cases seemed to indicate, or at least draw attention to, a particular [location]" (Tanner and Byrne (1996, p. 169).

These findings raise two relevant issues; first, that apes may engage in an inconspicuous, multi-faceted form of body pointing (rather than using a specialised referential signal, such as an extended arm and/or finger: e.g., Menzel 1973), or point with their eyes, by using gaze as an intentional referential signal (de Waal 2001). Second, while the question remains, as to whether the apes in Menzel's studies behaved to encourage others to act upon the target (imperative intention) or to influence their mental states (declarative intention, as defined in more recent formulations, see above), *or* to evoke an attentional and/or emotional reaction, as reflected in overt manifestations (social referential pointing intention), the results suggest that apes may, under some circumstances, direct conspecifics to hidden objects to, minimally, elicit an attentional response.

1.5.5 The morphology of non-verbal deixis

Pointing is broadly defined as a communicative movement that projects a vector from the body to indicate a direction, object, event or location (Kita 2003). Researchers of non-primates (e.g., dogs) have typically deployed a broad definition of deixis (the ability to locate, a specific entity or location for another), consisting of (i) an attention-getting and (ii) a directional component (Miklósi *et al.* 2000), while studies of humans and other primates (with arms and hands!) have often used a more narrow definition of simultaneous extension of the arm and index finger, with the remaining fingers curled under the hand (e.g., Franco & Butterworth 1996; Butterworth 2003; Povinelli *et al.* 1997, 2003). Butterworth and colleagues have advocated a distinction between children's referential gestures with and without index finger extension, with only the former reflecting an understanding of the psychological states of the communicative partner (Franco & Butterworth 1996)[21], and suggested that the arm and pointing hand have become specialised for referential communication, due to salience and usefulness in taking attention to the 'peripheral' (Butterworth 2003). While longer levers *are* superior in terms of conspicuousness and reduction of the distance between the pointer and indicated entity, and index fingers exceed other digits in terms of attention directing efficiency (Ariga & Watanabe 2009)[22], experiments into attentional shifts evoked by various hand gestures, however, suggest no advantage of experimentally manipulated longer versus shorter fingers (ibid.).

[21] The authors argued that while human whole-hand points serve to request objects, or actions on objects, index finger points serve to *comment* (Franco & Butterworth 1996; Butterworth 2003).
[22] Ariga & Watanabe (2009) examined the functional significance of index finger extension by studying the efficacy of different manual pointing gestures (fist with no finger extended, index

In human interaction, referential index finger pointing is ubiquitous, and has been cast as a biologically engendered (Povinelli & Davis 1994), universal from of human reference that reflects neurobiological adaptations, unique to the human lineage (Butterworth 1995). The gesture is widely considered independent of social transmission, which is supported by its cross-cultural stability (Eibl-Eibesfeldt 1989) and ability to elicit automatic shifts of attention (Ariga & Watanabe 2009) in a manner similar to that found in comparable gaze following paradigms (Emery *et al.* 1997). Despite the prevalence of index finger pointing in the West, and the consequent typical inclusion of index finger extension in the definition of pointing, manual pointing, however, differs cross-culturally in function, semantics and types of referents indicated. The function typically ascribed in the West is cross-culturally, frequently and conventionally, achieved by other morphological forms of pointing, e.g., whole hand-, elbow-, head-, eye- and lip-pointing[23]. In multiple societies lip and index finger pointing coexist (e.g., Arrente, Awtuw & Ewe: see Wilkins 2003), and in some, index finger pointing is infrequent (Kuna and Awtuw) and purportedly non-existent (the Barai, Watam & Yimas populations of New Guinea), with its function subsumed in ubiquitous and conventionalised lip pointing[24]. The prevalence, dominance and, in several groups on one island, exclusivity of lip pointing, casts doubt on the hitherto untested assumption that other forms of deixis but index finger pointing are inferior and less precise (as suggested by e.g., Hewes 1981 & Butterworth 2003). Individuals in these cultures most probably neither lack, nor have a different understanding of deixis and referential intent.

Moreover, human declarative gestures have different semiotic (including semantic) features, suggesting that pointing encompasses multiple or additive phenomena. Within for example the culture of Naples, Italy, different forms of manual pointing carry different semantic

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finger extended, little finger extended). All gestures triggered automatic attentional shifts towards the pointing direction, in a manner similar to that found in comparable gaze following paradigms (Emery *et al.* 1997), however the index finger point produced a larger cueing effect, leading to the overall suggestion that the processing of hand gestures form part of a primitive orienting reflex. Whether index finger advantage in modulating reflexive attention has a genetic or ontogenetic origin (as proposed by Butterworth [1998], who suggested that the habitual use of pointing gesture shapes the brain) remains unknown.

[23] Lip pointing consists of quickly shifting the eyes toward an intended entity, and raising the eyebrows and head, during which the mouth is first opened, and then closed with the lower lip thrust outward from the face (e.g., Wilkins 2003).

[24] Absence of index finger pointing has been reported for the Yimas and Watam New Guinean populations (Foley, reported by Wilkins 2003), and failure to understand the referential intent typically inferred from deictic index finger points for the Barai: "The Barai [of Papua New Guinea] were confounded when Olson used index-finger points with respect to objects as a means for getting names for them" (pers. com. with ethnographer Mike Olson reported by Wilkins 2003, p. 176).

connotations that are related to the way the object referred to, is presented within the speaker's dialogue (Kendon & Versante 2003).[25] Six types of declarative pointing (including three whole-hand points, morphologically similar to chimpanzee whole-hand pointing gestures) have been identified, distinguished by the shape of the hand and rotation of the forearm, and associated semantic differences in meaning, leading to the suggestion that the pointing type provides information, as to how a speaker wishes an indicated object to be considered (Kendon & Versante 2003). If so, gestural deixis can function as more than an indicating tool, with its exact meaning interpreted on the basis of features that accompany the directional component.

The plurality of form, and the in some cases subtle, morphological differences in pointing gestures and associated changes in meaning, and the apparent lack of use and/or understanding of the referential intent of index finger pointing among the multiple human groups, have implications for the study of non-human comprehension and production of referential gestures. If the form of pointing gestures is culturally specified (as per the suggestion that the gesture is acquired through imitation: Scassellati 1999; Brinck 2004), and not universally understandable, the implication is that no single phylogenetic and ontogenetic laws can be presupposed from the prevalence (and possibly, comprehension) of particular forms of deixis (Wilkins 2003). If index finger pointing is a socially transmitted gesture, and declarative gestures implicate the same cognitive capacities as true imitation (e.g., Brinck 2003, 2004), the limited imitative abilities of chimpanzees (e.g., Whiten *et al.* 2004) could be argued to underlie the scarcity/absence of chimpanzee declarative gestures. Nonetheless, the near universality of the human index finger pointing gesture, and the emergence of declarative index finger pointing in early human ontogeny (at a time when the ability to engage in full and 'true' imitation has not developed), raises serious doubt as to the claim that declarative gestures implicate the same cognitive abilities as true imitation (e.g., Brinck 2003).

If a species has the ability to produce referential deixis, it should (irrespective of how inconspicuously the capacity may be expressed) be capable of manipulating conspecific attention as efficiently, as a human pointing with the index finger (e.g., Menzel 1973).[26] Thus,

[25] Kendon & Versante (2003) found that in Naples, whole-hand points serve to direct the attention of the addressee to something on account of its implication for the interaction. For instance, whole-hand points with the palm facing upwards, offer something for examination, while points with the palm oriented obliquely indicate the relationship between the indicated entity and the speaker's interlocutor.

[26] Indeed, this is supported by recent neuroimaging studies, showing that different forms of pointing (pointing manually, or with gaze) are grounded in a common cerebral network (i.e. both manual and ocular pointing activate the posterior parietal and frontal cortecies, see Løvenbruck *et al.* 2009)

research into ape production of nonverbal deixis should place less emphasis on arm (and finger) extensions (e.g., Menzel 1974), and look for behaviours in general that may function as deictic gestures. The key features of pointing lie in function and directionality, not morphology.

1.6 This study

Despite considerable attention to the 'enculturation hypothesis' (Call & Tomasello 1996), ontogeny and environment frequently receive short shrift in studies and conclusions drawn regarding ape social communication, where the behaviours of typically developing children are frequently compared with those of animals with rearing histories untypical of their own species. The vast majority of cognitive studies of ape social attention have been conducted with a few groups of apes, raised in close contact with humans, and who have participated in numerous experimental studies in joint attentional contexts (see Appendix 3). Ontogeny, however, is as important as phylogeny in the expression of phenotypic characters, and (perhaps, particularly) also of cognitive-communicative skills that develop in social contexts. For example, cooperation, emotional engagement and joint attention behaviours vary in chimpanzees as a function of early experience, and differ across individuals who are raised with cohorts in standard nursery conditions, experience a stressful first 4 weeks of life (after which they were removed from their mothers for safety reasons), and those who have received an additional four hour daily human caregiver interaction (Bard & Gardner 1996; Bard *et al.* 2005; van Ijzendoorn *et al.* 2009), suggesting that care should be exercised when attributing socio-cognitive performance to species differences, without careful consideration of ontogeny.

This research program had three main aims. First, (i) I wished to assess the conspecific attention following skills of experimentally naïve bonobos and orangutans, for whom little systematic information exists (see, however, Kaplan & Rogers 2002 for two observations of conspecific orangutan gaze following, and Pitman & Shumaker 2009 for a recent study of conspecific gaze following). Moreover, while chimpanzee conspecific attention following has been demonstrated under conditions where multiple observed individuals have been induced to raise their heads at an 80° angle to look towards food presented in an observation tower (Tomasello *et al.* 1998), and in more subtle interactions between humans and chimpanzees with substantial experimental experience, little is known about its occurrence during every-day interactions with conspecifics, towards locations where no interesting events (such as human

presence) typically occur. Primates may be more interested in what conspecifics than humans attend to, and to motivate joint attention behaviours, subjects in the present research program were therefore tested in naturalistic settings during interactions with conspecifics.

Second, (ii) I wished to test the hypothesis that experimentally naïve bonobos, chimpanzees and orangutans are able and inclined to geometrically follow the attention of conspecifics (rather than humans) around barriers in non-competitive situations. The decision to test this emerged during the analysis of data from the ape population first tested (chimpanzees at Copenhagen zoo). 'Direct attention following' and 'geometric attention following' were therefore not designated conditions from the study outset, but emerged out of the opportunistic nature of the experimental set-up and data collection, which sometimes required the animals to locomote around a barrier, so as to co-orient to conspecific visual attention. In trials conducted with other chimpanzee populations, bonobos and orangutans (which were tested using the same basic methodology, detailed in Chapter 2), I sought an even distribution of 'direct' and 'geometric' trial conditions. Given the rarity of opportunities to conduct trials (which had to fulfil a number of requirements), there was, however, some variation in the relative proportions of 'direct' and 'geometric' trials across the species.

Visual replicas of predators (e.g., leopards, eagles and snakes) have been presented to a number of species (e.g., chimpanzees: Menzel 1974; vervet monkeys, *Cercopithecus aethiops*: Cheney & Seyfarth 1985; fowls, *Gallus gallus*: Evans & Evans 2006; Barbary macaques: Roberts *et al.* 2008; Putty-nosed monkeys, *Cercopithecus nictitan martini*: Arnold & Zuberbühler 2008; Campbell's Monkeys, *Cercopithecus campbelli*: Ouattara *et al.* 2009) and have, in some cases, elicited functionally referential vocalisations and directional behaviours towards the replicas, that conspecifics have used to guide their own behaviour. The question of the animals' consideration of others' visual access to the replicas, and potentially intentional re-direction of conspecifics to the replicas, however, remains debated, and have widely been dismissed. One way to disentangle intentional signals from the unintentional, adventitious, stimulus-directional cues that frequently accompany fear responses is to present objects that evoke interest and/or uncertainty, rather than fear or want, and record if behaviours (and combinations thereof) differ as a function of conspecific presence and visual attention to the objects.

While social referencing studies have presented apes with non-frightening, novel objects, the mother's/caregiver's visual access to the stimulus has typically obviated any need for the infants to actively redirect the mother's/caregiver's attention to the object. The one social referencing study, which has included trials, in which the infant saw a novel (though potentially

frightening) object before its mother did (macaques: Roberts *et al.* 2008), did not examine the presence of attention getting behaviours, and neither intentional nor adventitious (functional) attention directing. To fill this gap in the literature, the present study presented chimpanzees, bonobos and orangutans with a novel stimulus of potential but ambiguous significance (a laser image or pattern), predicted to evoke interest rather than fear or want, so as to test if the apes would lead conspecifics to detect the stimulus. The third (iii) aim of this research program was therefore to identify possible behaviours that consistently act as cues triggering intra-specific attention following, and test if the apes engaged in directional signalling that, although not necessarily corresponding to hand-pointing, might be meaningful to the animals. That is, whether the apes might engage in non-verbal deixis when during interactions with conspecifics.

CHAPTER 2: Attention following in chimpanzees

Summary

Following others' attention is an adaptive skill that enables individuals to obtain and share useful information. This study investigated whether chimpanzees follow conspecific attention to distal locations. Ten adult and three infant chimpanzees were presented with a novel visual stimulus to test if they would lead an ignorant conspecific to detect it under two experimental conditions. In one, the conspecific faced the communicator, while another required the communicator to first attract the attention of a non-attending conspecific. Five control conditions tested the likelihood that conspecifics detected the stimulus on their own, and the influence of conspecific presence, and one examined audience effects. Adult chimpanzees failed one control condition (which however showed the right tendency), yet all comparisons support the notion of attention re-orientation in response to both adult and infant conspecific behaviour.

2.1 Introduction

A central issue in the study of primate communication is the extent to which individuals share the attention of others. Chimpanzees follow the gaze of humans to distal locations outside their own visual fields, looking behind barriers and themselves in the process, in a manner suggesting that gaze following is not an inflexible stimulus-response (Povinelli & Eddy 1997; Tomasello *et al.* 1998; Call *et al.* 1998; Tomasello *et al.* 1999; Bräuer *et al.* 2005). Chimpanzees also follow the attention of conspecifics under conditions where other individuals have been induced to raise their head at an 80° angle (Tomasello *et al.* 1998; Pitman & Shumaker 2009) and in competitive contexts (Hare *et al.* 2000; Hare *et al.* 2001). Importantly, however, while chimpanzees show flexible and sophisticated cognitive abilities in tasks involving *competition,* these are typically not expressed in cooperative contexts when a helpful a human or conspecific provides gaze or other directional cues about the location of hidden food (Povinelli *et al.* 1996; Tomasello *et al.* 1997; Povinelli *et al.* 1997; Call *et al.* 1998; Itakura *et al.* 1999; Povinelli &

Bierschwale 1999; Call *et al.* 2000; Hare & Tomasello 2004). Recently, however, researchers have argued that environmental and methodological differences greatly influence chimpanzees' (and other great apes') use of declarative human gestures in the object-choice task (Mulcahy & Call 2009; Lyn 2010), and have shown that chimpanzees (and bonobos) reared in socio-linguistically complex environments, do deploy proximal human points to a baited container (2-10 cm distance to the container), when these are accompanied by additional cues, such as a vocalisations and gaze alternation between the subject and the indicated container (Lyn *et al.* 2010).

2.2 Study 1: Adult chimpanzees

2.2.1 Introduction

The study had two aims. First, chimpanzee conspecific gaze-following has been demonstrated under conditions where the observed individual has been induced to raise its head at an 80° angle to look towards food presented in an observation tower (Tomasello *et al.* 1998) or to a location approx. 2m above and immediately behind the subject, and indeed in more subtle interactions (involving less conspicuous head movements between humans and chimpanzees with substantial experimental experience (Bräuer *et al.* 2005). Yet, little is known about its occurrence during more naturalistic interactions with conspecifics. Second, the experiment tested the hypothesis that experimentally naïve chimpanzees are able and inclined to geometrically follow the gaze of conspecifics (rather than humans) in a non-food related and non-competitive context.

Participants were tested in naturalistic settings during interactions with conspecifics and presented with a laser stimulus of potential, but ambiguous significance, predicted to evoke interest rather than want or fear. One individual in a dyad (the communicator) was presented with a moving laser pattern or image to test if a conspecific (termed, 'the target') would co-orient to the communicator's attention to the stimulus under two experimental conditions. In the first condition the target animal faced the communicator who viewed the stimulus, while in the second condition, it faced away from the communicator. The first condition tested attention following, while the second required the communicator (by some means, adventitious or intentional cues) to first attract the conspecific's attention. Five control conditions examined whether conspecifics detected the stimulus on their own and the influence of the presence of conspecifics. It was predicted that there would be a difference between targets' looks to the

stimulus area during a 30s pre-stimulus and 30s stimulus phase in experimental but not control trials, and a difference between targets' looks to the stimulus area during the 30s stimulus phases of experimental and control trials. In attempt to distinguish between target looks to the stimulus area occurring by chance and due to expectation of a point of interest (as a consequence of a conspecific looking to the stimulus area), the duration of time that targets spent looking to the stimulus area during the pre-stimulus and stimulus phases of experimental trials was recorded.

2.2.2 Methods

2.2.2.1 Participants

Participants consisted of ten adult chimpanzees (*Pan troglodytes spp.*), four males and six females ranging from 10 to 34 years of age (mean = 24.40, s.d. = 7.55, Table 2.1). Five individuals were previously housed at a medical facility, yet none had previously participated in behavioural experiments and all were experimentally naïve. Initially, the study was designed for sixteen individuals, but six individuals were excluded from the analysis. One died during the course of data collection and five spent insufficient time alone in the experimental enclosures to receive sufficient control trials. Moreover, one individual (Jonnie, Whipsnade Zoo, see Table 2.1) served only as a 'target' individual in experimental trials, but was otherwise omitted from the study, due to time restrictions.

Table 2.1: Chimpanzee participants.

Individual	Sex	Date of birth	Age	Rearing history	Zoo
Carl	M	18-07-87	19	Parent	Copenhagen
Cindy	F	27-10-87	19	Parent	Copenhagen
Coco	F	04-06-73	34	Unknown	Whipsnade
Jolly	F	21-10-77	30	Hand	Twycross
Jonnie	M	20-05-09	41	Unknown	Whipsnade
Kip	M	22-04-76	31	Unknown	Twycross
Mati	F	16-10-87	19	Parent	Copenhagen
Olga	F	12-08-84	22	Parent	Copenhagen
Trunte	F	1970	36	Parent	Copenhagen
William	M	30-06-82	15	Unknown	Twycross
Yoran	M	31-10-87	19	Parent	Copenhagen

Husbandry

All chimpanzees were housed in social groups between two and 13 individuals in enclosures separated from the public areas by large windows.

Copenhagen Zoo

The group at Copenhagen Zoo comprised of eight adult chimpanzees and three infants. Six of the eight adults (see Table 2.1) participated in the study, while two were excluded; One died during the course of data collection and one spent insufficient time alone in the experimental enclosures so as to receive sufficient control trials. The animals had access to four adjoining indoor enclosures (Figures 2.1 & 2.2), of which one was secluded from public view (Figure 2.1, enclosure 4). The chimpanzees had auditory access to the public areas, as enclosures were separated from these by a 4 m high glass window with a 2 m opening towards the ceiling. Enrichment consisted of trees, climbing structures, ropes, an artificial termite mount and a Plexiglas structure, from which food could be extracted with sticks. In addition, the keepers provided the chimpanzees with leafy branches, animal carcasses and food frozen in water. Two individuals (of which one was excluded from the data pool) regularly engaged in regurgitation and the eating of faeces, yet no other stereotypic behaviours were observed. The exhibit received the majority of its visitors between the hours of 10.30-14.00, during which school children frequently engaged in calm interactions with primarily the infants and one old female (excluded from the data pool).

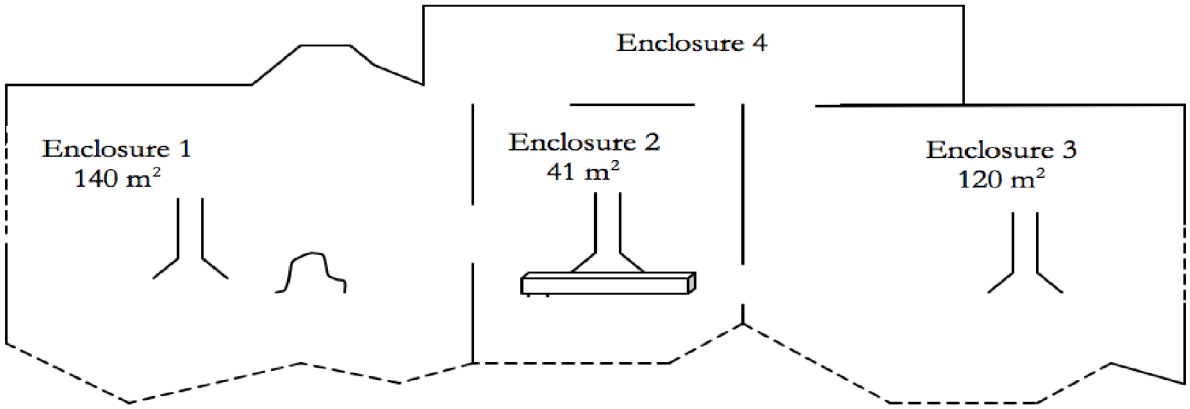


Figure 2.1: Enclosures at Copenhagen Zoo. Dotted lines indicate windows to public areas and illustrations depict a termite mound (enclosure 1), a Plexiglas structure (enclosure 2) and trees.

Figure 2.2: Experimental enclosures at Copenhagen Zoo (enclosures 1-3).

Twycross Zoo

The group at Twycross Zoo comprised of seven adult chimpanzees, of which three participated in the study (i.e., received trials as both 'communicators' and 'targets'). The remaining individuals were excluded, as they spent insufficient time either alone and/or as part of a dyad in the experimental enclosures to receive sufficient and important control trials. The apes had access to one outdoor enclosure and two adjoining indoor enclosures separated by a sliding door and wire-mesh (Figures 2.3 & 2.4). Neither the indoor nor outdoor enclosures provided a place for the chimpanzees to be out of view of the public. The indoor enclosures contained a large mirror, a metal climbing structure, hanging baskets, rubber ropes, a car wheel and a television screen (tuned to the BBC). In addition the keepers provided the apes with a variety of enrichment in the form of plastic bottles, cloth and boxes made from cardboard and plastic. Between the hours of 11.00-14.00 several family or school groups observed the chimpanzees at any one time, and the exhibit was exposed to more visitors and noise than those at either of the other zoos. Members of the public frequently attempted to engage with the chimpanzees, which often resulted in animals charging, banging on, or throwing items at the windows. Two chimpanzees engaged in seemingly more frequent and more types of stereotypic behaviour (rocking, glass-licking, the eating of faeces and regurgitation) than individuals at either of the other zoos.

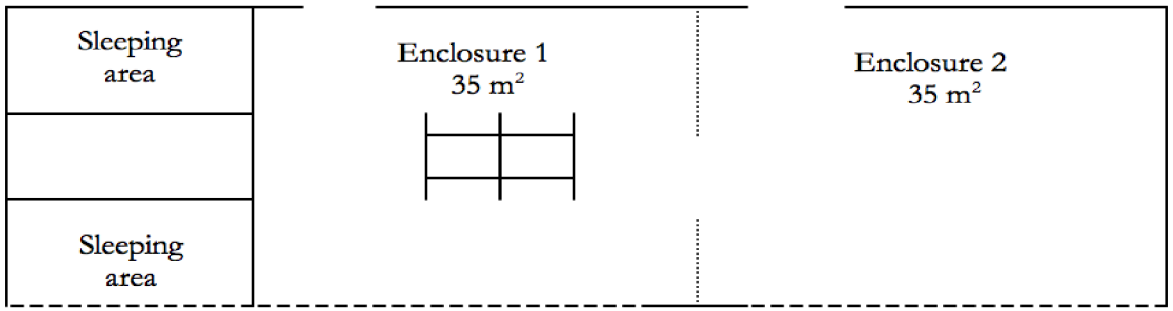


Figure 2.3: Inside enclosures at Twycross Zoo. Dotted lines indicate windows to public areas and the illustration a metal climbing structure (enclosure 1).

Figure 2.4: Experimental enclosures at Twycross Zoo.

Whipsnade Zoo

The group at Whipsnade Zoo comprised of two adult chimpanzees that had recently transferred from London Zoo and were therefore separated from conspecifics. One individual (Coco) participated in the experiment (i.e., received experimental and control trials, serving both as a 'communicator' and 'target', see following sections for clarifications of the terms), while the individual with whom it was co-housed (Jonnie, male, 41 years) served only as a 'target' individual in experimental trials (see descriptions of the conditions in following sections and Table 2.3), but was otherwise omitted from the study, due to time restrictions. During the day the chimpanzees were housed in one large indoor enclosure, in which they had continual visual and auditory access to one another (Figures 2.5 & 2.6). Enrichment consisted of logs, a metal climbing structure, ropes and cardboard boxes. The exhibit received few visitors and no stereotypic behaviours were observed.

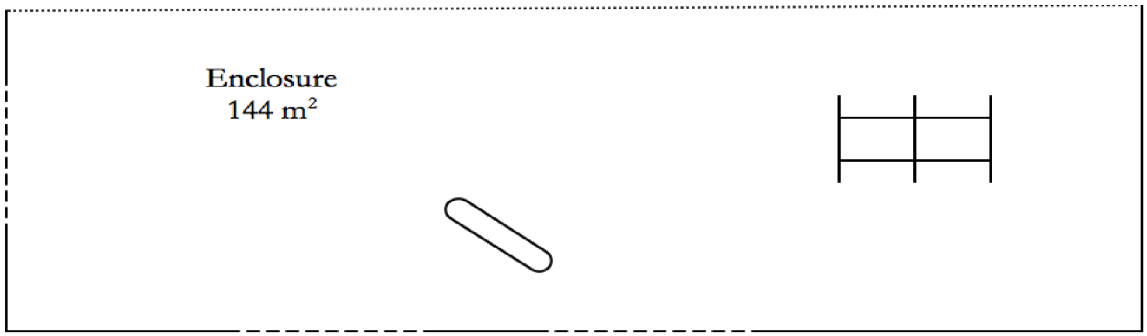


Figure 2.5: Experimental enclosure at Whipsnade Zoo. Large dotted lines indicate windows to public areas and illustrations a wooden log and a climbing structure.

Figure 2.6: Experimental enclosure at Whipsnade Zoo.

2.2.2.2 Data collection

The chimpanzees were tested between August 2004 and July 2007 during a total of 1,390 hours of observation time. Trials were conducted outside opening hours and at times when there were few members of the public present, between the hours of 6.30-10.30 and 14-19.30 at Copenhagen Zoo, 7.30-11.00 and 14-16 at Twycross Zoo and 8.30-16.00 at Whipsnade Zoo. Testing took place primarily in inside enclosures. Ninety-eight percent of the trials (125 trials) were conducted inside, while 2 % (3 trials) were conducted outside. In none of the trials conducted outside did the participants view the stimulus (see Appendix 1 for pictures of the outside enclosure). The experiment was recorded by two camcorders (Panasonic NV-GS120 and Sony DCR-HC40/DCR-PC55E). The miniDV videotapes were digitised into IMovie on a Macintosh IBook and converted into QuickTime files, from which the individuals' looks to the stimulus area during the pre-stimulus and stimulus phases were scored and transferred into an Excel spreadsheet.

2.2.2.3 Design, materials and procedure

The experiment used a repeated measures design with two experimental and four control conditions. The apes were tested during normal interactions with conspecifics; opportunistically, when the inter-animal distance and spatial constellations required for the trials were met. The experimenter projected a visual stimulus into the participants' enclosure; a red or green laser dot that, when moved, produced a light pattern within an area of approx. 0.5m^2 (using a commercial laser pointer, OnPoint GR532: red: 635 nm; green: 532 nm, power output: 5 mW, laser-point diameter at 4m distance to display surface: approx. 2cm, Figures 2.7a and 2.7b). Laser beam invisibility was established in a pilot study, where the stimulus was projected across the line of sight of participants to a point outside their visual fields (N = 8). No chimpanzee interrupted its behaviour or showed signs of detecting the beam. Four participants (housed at Whipsnade and Twycross zoo) received all trials with a more powerful green laser (3b laser; Extreme Fusion: 532 nm; power output: 125 mW, point diameter at 4m distance: approx. 3cm) with an optical diffractive element attached, so it produced an image of an insect. The diffractive element weakened the stimulus brightness, but increased the size of the stimulus to approx. 0.5 m^2 (Figure 2.7c). Prior to the study St Andrews University provided extensive training in the use of laser pointers. Care was taken to ensure that the apes never looked directly into the laser pointer, and that the laser beam was not aimed at, or displayed anywhere on the bodies of individual animals.

(a) (b) (c)

Figure: 2.7: Stills of stimuli; (a) red laser stimulus (a dot) moved so as to produce a moving light pattern of approx. 0.5 m^2 (a line, rather than the pattern is visible in the still), (b) green pattern stimulus, (c) image stimulus.

The stimulus was projected so that it was visible to the communicator for 30s, but removed earlier if the target looked to the stimulus area. To preserve the novelty value of the stimuli (for targets who also served as communicators, see below for further details), it was removed immediately after a target reoriented towards it, but before the stimulus area came within the target's 'open' or 'peripheral' field of vision (see Figure 2.12). If the stimulus fell within the target's 'open' field of vision, the trial was scored as the target having oriented to the stimulus. To prevent detection of the origin of the stimulus, it was temporarily removed if a participant looked towards the experimenter (located in the public area). To ensure consistent stimulus projection across trials, the stimulus was removed for 5s in all trials, due to either natural interruptions (a brief removal to prevent detection of the stimulus origin, if a participant looked towards the experimenter), or during 5 1s intervals during the last 10s of stimulus presentation. The duration of the pre-stimulus and stimulus presentation phases considered for analysis was 30s, the latter commencing at the beginning of stimulus presentation. The stimulus was projected from the public areas onto 27, 12 and 4 different locations in the experimental enclosures at Copenhagen, Twycross and Whipsnade Zoo, respectively (Figures 2.8-2.10).

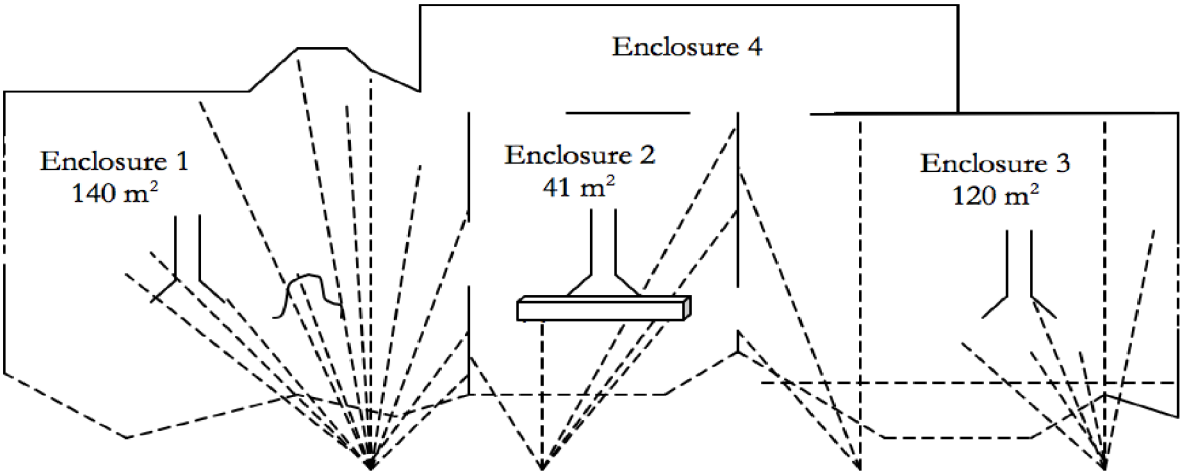


Figure 2.8: The use of the experimental enclosures at Copenhagen Zoo. Dotted lines indicate stimulus projection points at 27 locations, projected from the public areas.

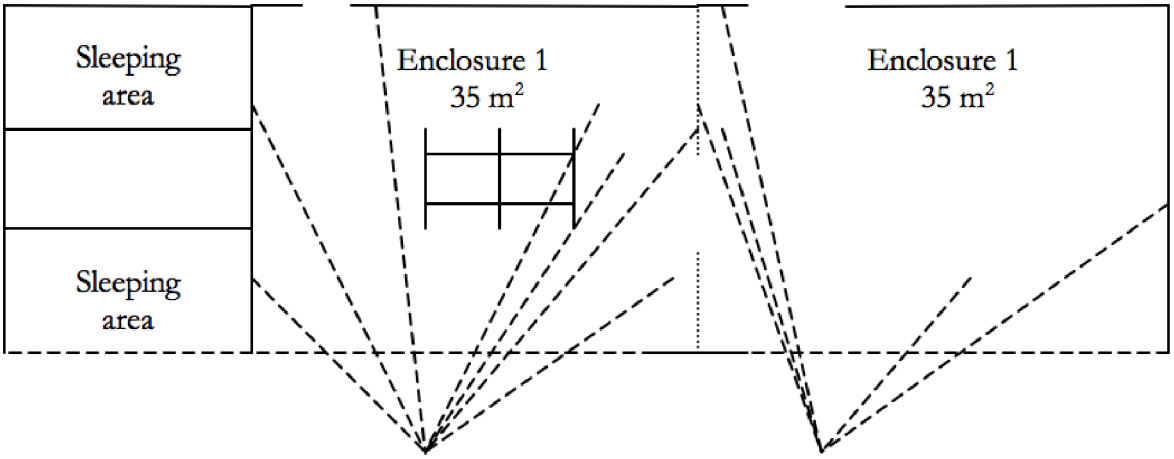


Figure 2.9: The use of the experimental enclosures at Twycross Zoo. Dotted lines indicate stimulus projection points at 12 locations.

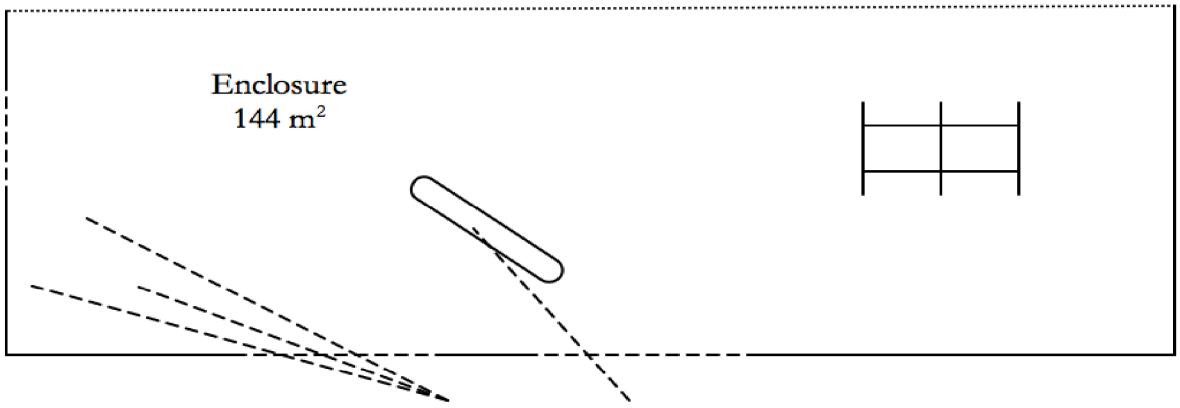


Figure 2.10: The use of the experimental enclosures at Whipsnade Zoo. Dotted lines indicate stimulus projection points at 4 locations.

Experimental Condition 1: Target Faces Towards Communicator (Experimental-Towards)

The condition was designed to test if targets followed the gaze of a conspecific, during naturalistic interactions, to a point where no interesting events frequently occurred. A communicator and target faced each other at a 1-5m distance during a minimum of 80% (24s) of the 30s pre-stimulus phase and at the start of the stimulus projection. Relative head and gaze orientation of the animals were divided into 'open' (facing directly towards), 'peripheral' (facing sideways to), or 'closed' (one's back to) the other animal. The 'closed' category included cases where an environmental feature obstructed the target animal's view of the communicator animal. A target was defined as facing a communicator when its 'open' visual field was oriented towards the communicator's 'open' or 'peripheral' visual field (Figures 2.11 and 2.12), and as looking to the stimulus location when this fell within the target animal's 'open' field of vision (Figure 2.12).

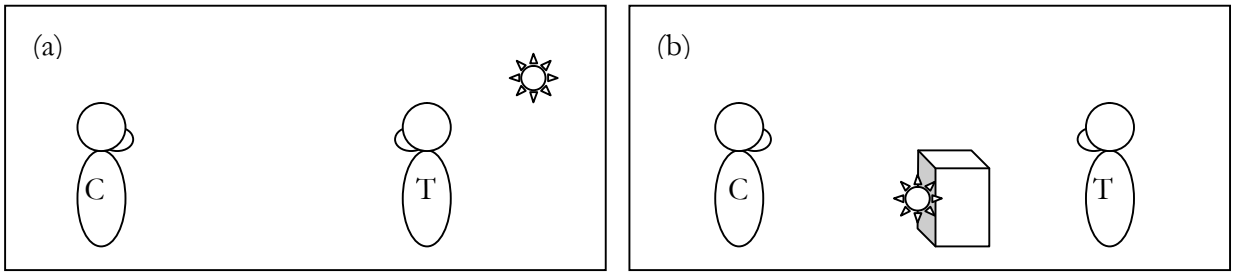


Figure 2.11: *'Target (T) faces towards communicator' (C).* (a) Target (T) is required to turn around, so as to look to the stimulus. (b) Target is required to locomote around an obstacle, so as to look to the stimulus.

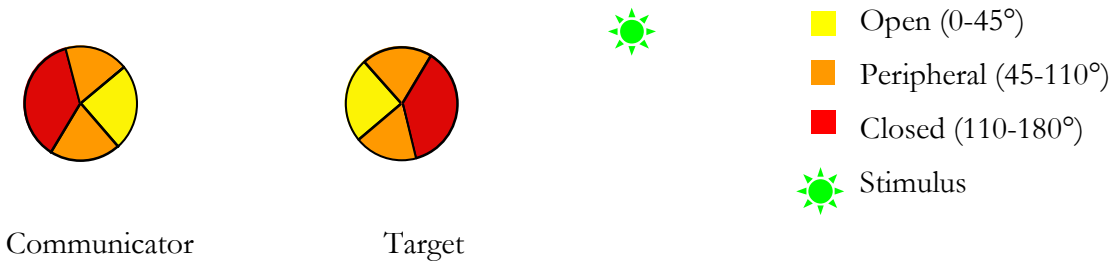


Figure 2.12: Animal orientational constellation at the start of the *'Target faces towards communicator'* condition. Yellow, orange and red colours indicate visual fields measured from the saggital plane between the animals' eyes.

Experimental Condition 2: Target Faces Away from Communicator (Experimental-Away)

This condition was designed to test if, when a target was unable to detect any visual behaviour exhibited by the communicator, the communicator would attract the attention of the target, and (inadvertently or intentionally) lead the target to look to the stimulus location. That is, if the communicator considered the target's visual attention, and upon viewing the stimulus, behaved differently as a function thereof. The condition was identical to the '*Target faces towards communicator*' condition, except that the target faced *away* from the communicator during a minimum of 80% (24s) of the 30s pre-test phase and at the start of the stimulus projection. A target was defined as facing away from a communicator when the back of its head ('closed' visual field) was oriented towards the communicator's 'open' or 'peripheral' visual field, or if the communicator was occluded from the target's view by an environmental obstacle (Figures 2.13 and 2.14).

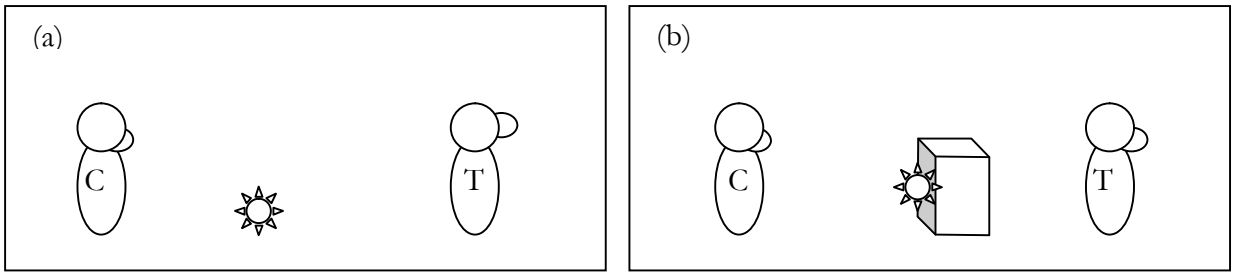


Figure 2.13: '*Target (T) faces away from communicator' (C).* (a) Target (T) is required to turn around, so as to look to the stimulus. (b) Target is required to locomote around an obstacle, so as to look to the stimulus.

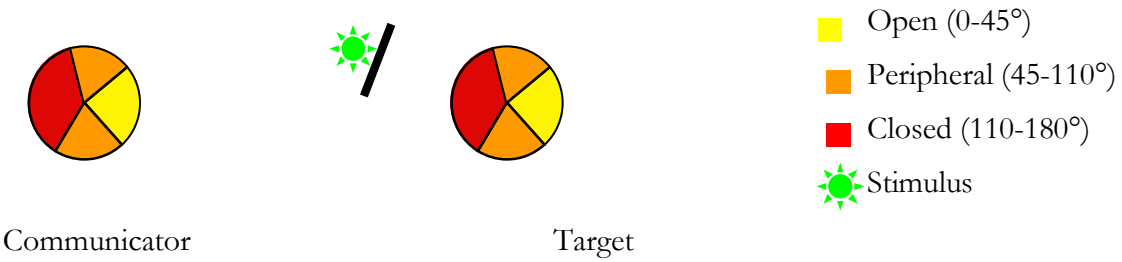


Figure 2.14: Animal orientational constellation at the start of the '*Target faces away from communicator*' condition. Yellow, orange and red colours indicate visual fields measured from the saggital plane between the animals' eyes.

Control Conditions 1 and 2: No Stimulus - Target Faces Towards/Away from Communicator (No Stimulus-Towards & No Stimulus-Away)

The '*No Stimulus*' control conditions were identical to the experimental conditions, (Figures 2.11 and 2.13), except that no stimulus was projected (Figure 2.15). At the start of a trial the experimenter aimed the laser pointer and specified vocally where the stimulus would have been projected (a location similar to that in an experimental trial). Targets' looks to the stimulus location were recorded during the 30s pre-stimulus and stimulus phases. The 30s pre-stimulus phase of '*No Stimulus*' conditions provided the same baseline measure as the pre-stimulus phase of *experimental* trials (i.e., participants were in the same orientational constellation, and no stimulus was projected). The stimulus phase of the '*No Stimulus*' conditions, however, contained the added factor that the experimenter aimed (though did not project) the stimulus at a specified location, thus providing a 'Clever Hans Control', as changes in experimenter body tension, and/or movement of the stimulus projector might provide inadvertent cues as to the location on which the stimulus was aimed. The '*No Stimulus*' conditions thus (a) measured the probability that targets looked to the stimulus location in the absence of the stimulus, while in the presence of another individual (as the presence and/or orientation of a conspecific might influence scanning frequency and thus looks to the stimulus area [identical to the function of the pre-stimulus phase of *experimental* conditions), (b) provided a baseline for comparison of the communicators' behaviour during the experimental conditions, and (c) tested for possible inadvertent cuing by the experimenter (the 'Clever Hans Effect').

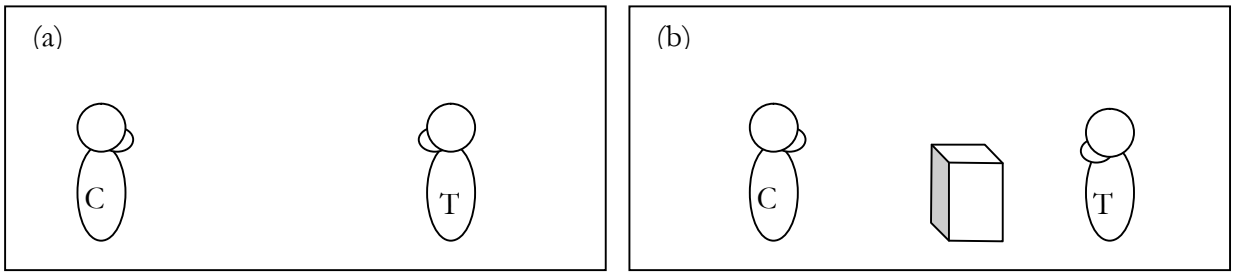


Figure 2.15: '*No Stimulus – target faces towards communicator*'. (a) The stimulus is aimed on a location behind the target (T). Target is scored as looking to the stimulus location, if it turns, and the stimulus location falls within its 'open'/'peripheral' field of vision. (b). The stimulus is aimed on the left side of the obstacle. Target is scored as looking to the stimulus location, if it locomotes around the obstacle, and the stimulus location falls within its 'open'/'peripheral' field of vision.

Control Condition 3: Target Alone

This condition provided a baseline-measure of chance stimulus detection, by testing the likelihood that a target looked to the stimulus by itself and chance (i.e., looked to the stimulus location in the absence of a communicator potentially providing information as to the presence of the stimulus). The stimulus was projected to a point outside the view of a target alone in an enclosure, in a way similar to that in the experimental conditions (Figures 2.11 and 2.13), but with no communicator present (Figure 2.16).

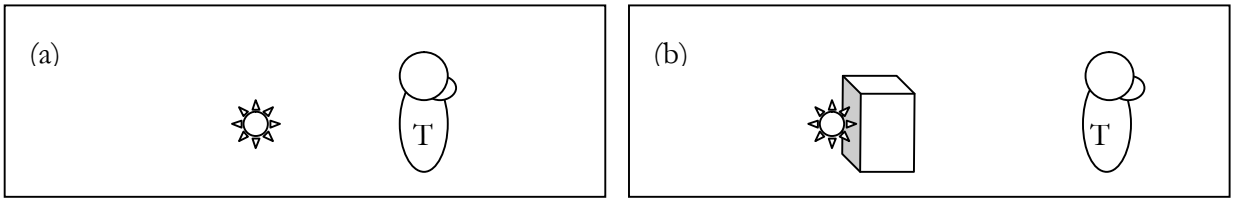


Figure 2.16: '*Target Alone*'. (a) Target is scored as looking to the stimulus location, if it turns around. (b) Target is scored as looking to the stimulus location if it locomotes around the obstacle and the stimulus location falls within its 'open'/'peripheral' field of vision.

Control Condition 4: Target and Ignorant Communicator

This condition tested the probability of targets detecting the stimulus by chance when accompanied by a communicator, ignorant as to the presence of the stimulus. That is, it tested chance detection (as the '*Target Alone*' control), but with the added consideration that scanning rates (and thus chance stimulus detection) might increase as a consequence of conspecific presence. Thus, this condition was predicted to provide a more conservative measure of chance stimulus detection in the absence of a communicator viewing the stimulus than '*Target Alone*'. The stimulus was projected to a point outside the view of a target and communicator (Figure 2.17). If the communicator oriented towards the stimulus, it was removed before it fell within the animal's peripheral field of vision and the trial abandoned. If the target oriented towards the stimulus (i.e., if the stimulus fell within the target's 'open' field of vision), the stimulus was also removed, but the trial scored as the target having looked to the stimulus area.

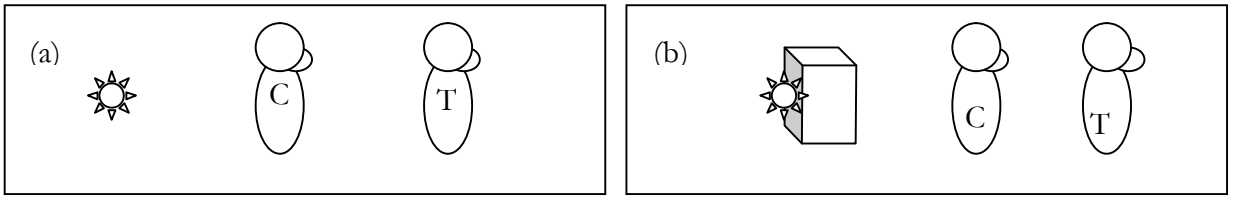


Figure 2.17: '*Target and Ignorant Communicator*'. (a) Target is required to turn around, so as to look to the stimulus. (b) Target is required to locomote around an obstacle to look to the stimulus.

Control Condition 5: Communicator Alone (Audience effect, COM)

This condition tested if behaviours produced by communicators in experimental trials (ground slapping, stimulus directed behaviours, etc.) reflected a heightened state of arousal or possessed a communicative function, i.e., if the communicator took conspecific presence into account. The stimulus was projected onto a location within the 'open' visual field of a lone communicator in a manner as during an experimental trial (Figure 2.18). The communicator was allowed to examine the stimulus for 30s, yet the stimulus was removed before 30s had elapsed if a) the communicator left the enclosure, or b) a conspecific entered the enclosure. The communicators' behaviour in *experimental* and *control* conditions are examined in Chapter 3.

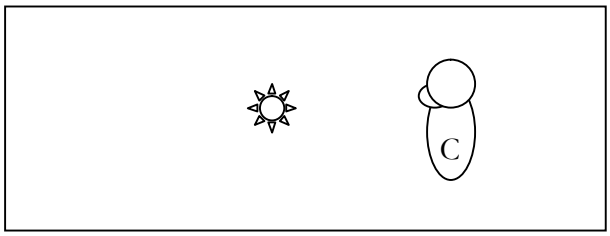


Figure 2.18: '*Communicator Alone*' condition.

Trials requiring targets to turn versus locomote to detect the stimulus

Seventy-eight percent (103 of 132) of experimental and control trials required targets to only *turn* around to look to the stimulus area, while 22% (29 of 132) required targets to first *locomote* around a structure (Table 2.2). 'Locomote' trials reduced adventitious stimulus detection, and experimental 'locomote' trials provided information about geometrical conspecific attention following. The two trial types were not designed conditions, but a result of the opportunistic nature of the experimental set-up and data collection. While all trials within the different conditions were analysed together, 'turn' and 'locomote' trials were also considered and analysed separately.

Table 2.2: Trials requiring targets to locomote around a visual barrier ('Locomote') and turn around ('Turn') to look to the stimulus area. The '*Experimental*' and '*No Stimulus*' conditions each consisted of two trial types (where targets faced either *towards* or *away* from the communicator at the start of stimulus projection).

Condition	**Percent**		**N**	
	Turn	**Locomote**	**Turn**	**Locomote**
Experimental	59	41	22	15
No Stimulus	76	24	29	9
Target Alone	90	10	36	4
Target and Ignorant Communicator	94	6	16	1
Total	78	22	103	29

2.2.2.4 Trial sequences

The conditions were presented sequentially in an order determined by means of Latin Squares technique and counterbalanced so that equal numbers of participants received a '*Communicator Alone*' trial before the first *experimental* trial, and *vice versa*. Each sequence consisted of 7 trials, two experimental- and five control conditions, with the '*Target Alone*' condition presented twice, to get a reliable estimate of the baseline detection-rate (Table 2.3). Five participants received two sequences and two received an additional trial sequence (for one participant, bar one experimental trial, i.e., the individual received all control trials). Three individuals received only one trial sequence. Two of these were housed at a facility (Twycross Zoo) with small inside enclosures, where dyads were rarely alone and inconspicuous stimulus projection hard-won. After more than 330 hours collecting data from these participants, I decided to include only one trial sequence for the individuals. Some targets with dependent offspring were rarely alone and at one facility (Whipsnade) a target could not be tested individually; for these individuals, '*Target Alone*' trials were substituted by '*Target and Ignorant Communicator*' trials (predicted to produce higher levels of scanning and provide a higher, more conservative baseline measure of adventitious stimulus detection in the absence of a communicator viewing the stimulus). For the individual at Whipsnade Zoo the '*Communicator Alone*' trial was excluded.

Table 2.3: Trial sequences and order of presentation. EXP = '*Experimental*', NOS = '*No Stimulus*', TAR = '*Target Alone*', TAR+ = '*Target and Ignorant Communicator*', COM = '*Communicator Alone*', T = Target faces *towards* communicator, A = Target faces *away* from communicator. Cph = Copenhagen Zoo, Tw = Twycross Zoo, Wh = Whipsnade Zoo. Coloured text indicates trials involving a stimulus and stimulus colour. Highlighted trials were not conducted.

Individual	Trial Sequence	1	2	3	4	5	6	7	8
Carl (Cph)	1	TAR	NOS A	EXP A	EXP T	TAR	NOS T	COM	TAR+
	2	COM	NOS T	TAR	NOS A	EXP T	TAR	EXP A	TAR+
	3	NOS T	TAR	COM	NOS A	EXP A	TAR+	TAR	EXP T
Yoran (Cph)	1	NOS T	TAR	NOS A	EXP A	EXP T	TAR	TAR+	COM
	2	TAR	COM	EXP A	TAR+	EXP T	NOS T	NOS A	TAR
	3	TAR	EXP T	NOS T	TAR	EXP A	TAR+	COM	NOS A
Cindy (Cph)	1	COM	NOS A	EXP T	TAR	NOS T	TAR	TAR+	EXP A
	2	TAR	NOS T	COM	EXP T	EXP A	NOS A	TAR	TAR+
Jolly (Cph)	1	COM	TAR	NOS T	TAR+	NOS A	EXP A	TAR	EXP T
	2	TAR	EXP T	TAR	NOS T	TAR+	NOS A	EXP A	COM
Marti (Cph)	1	NOS A	TAR	EXP T	COM	TAR	TAR+	NOS T	EXP A
	2	TAR	TAR	EXP A	TAR+	NOS T	COM	EXP T	NOS A
Olga (Cph)	1	EXP A	TAR	EXP T	NOS A	TAR	NOS T	TAR+	COM
	2	TAR	COM	TAR	EXP A	EXP T	NOS T	NOS A	TAR+
Trunte (Cph)	1	COM	NOS T	NOS A	EXP A	EXP T	TAR	TAR+	TAR
	2	EXP T	NOS A	TAR	COM	NOS T	TAR	TAR+	EXP A
Kip (Tw)	1	COM	TAR+	TAR	NOS A	EXP A	TAR+	EXP T	NOS T
William (Tw)	1	TAR	EXP T	EXP A	TAR+	TAR	NOS A	COM	NOS T
Coco (Wh)	1	NOS T	TAR+	NOS A	EXP T	TAR+	EXP A	TAR+	COM

2.2.2.5 Scoring and reliability

All trials were scored from videotapes. I coded whether the stimulus area fell within targets' 'open' field of vision during the pre-stimulus and stimulus phases, respectively, and a second coder coded 89% (118 of 132) of trials to assess inter-observer reliability (100% of experimental trials [N = 37] and 85% [N = 95] of a random selection of control trials). Statistical analysis of agreement was made using Cohen's Kappa, a measure of the degree of non-random agreement between ratings of the same categorical variable. There was 97% agreement between the coders on both the pre-stimulus and stimulus phases (Cohen's kappa = 88.87 = very good agreement; Altman 1991).

2.2.2.6 Statistics

For the data analysis I took into account that the conditions compared contained unequal numbers of observations due to (i) missing values (see Table 2.3), (ii) that some subjects received more trial sequences than others, and (iii) that conditions comprised of different numbers of trials (i.e., each trial sequence contained two *experimental* trials, two *'No Stimulus'* trials, three '*Target Alone*'/'*Target and Ignorant Communicator*' trials and one '*Communicator Alone*' trial). To overcome these constraints the data were analysed in two ways; (1) I used a repeated measures binomial logistic regression (fitted by the Laplace approximation) with a binomial error structure to test the likelihood of target animals looking to the stimulus location during the pre-stimulus and stimulus phases of experimental and control conditions, respectively ('*pre versus post*' control), and to compare looks to the stimulus area during the stimulus phases of experimental and control conditions. The binomial logistic regression is a generalised linear mixed model (GLMM), which offers the key advantage over other statistical techniques, that it takes into account repeated observations of the same individuals, by allowing one to include participant as a random factor in the model (Pinheiro and Bates 2000). Including individual identity as a random factor dealt with the issue of potential pseudo-replication of repeated measures and of unequal numbers of observations (and hence unequal contribution to the dataset) for different subjects. In addition, (2) the first trial that individual participants received in each of the conditions was analysed by means of non-parametric McNemar tests for repeated measures and nominal data. To prevent pseudo-replication of observations (e.g., by subjects contributing two observations to the analysis of collapsed *experimental* and *No Stimulus* measures [one trial in which they faced *towards* and one where they faced *away* from the communicator at the start of the stimulus phase, respectively], McNemar testes were used to analyse performance in the pre-stimulus and stimulus phases of only the first trial received in individual conditions.

Null-hypotheses were rejected at an alpha level of 5%, and all tests were two-tailed. GLMM were performed using the statistical software 'R' (2009 edition, R Foundation for Statistical Computing), all other statistics were carried out in PASW 18 and Microsoft Excel. Inter-animal distance was estimated by the number of adult animal body-widths between individuals, multiplying the number by 50 to convert it to centimetres.

2.2.3 Results

There was no significant difference between targets orienting towards red, green or image stimuli (*experimental* trials, Fisher's Exact test: N = 37, $p = 0.76$, control trials: N = 57, $p = 0.17$), and trials involving the three types of stimuli were therefore analysed together. Chimpanzees followed the attention of conspecifics to the stimulus in 50% (10 of 20) of experimental trials, 60% (6 of 10) and 40% (4 of 10), respectively, in trials where they faced *towards* and *away* from the communicator at the start of stimulus projection (percentage based on the first trial that communicators received in the two experimental conditions, Table 2.4a).

Communicators produced a visible behaviour (approached, extended a hand towards or touched the stimulus, alternated gaze between the stimulus and target, repositioned its body while looking to stimulus, or arrested current behaviour) in 80% (16 of 20) of experimental trials (percentage based on only the first trial that communicators received in the two experimental conditions). Conspecifics followed the communicators' attention in 78% (7 of 9, Table 2.4b) of experimental trials where conditions were comparable to those under which the intra-specific attention following of five primate species has been tested (Tomasello *et al.* 1998); That is, when (i) trials where the communicator appeared to ignore the stimulus were excluded (as judged by the absence of visible responses to the stimulus), and the communicator produced a visible behaviour while being within the targets' 'open' or 'peripheral' field of vision, (ii) targets faced *towards* the communicator at the start of stimulus projection, and (iii) were required to only turn around so as to co-orient to the communicator's attention (rather than first 'locomote' around a visual obstruction).

Table 2.4: Attention following. Percent cases of attention following in (a) all first received experimental trials, (b) first received experimental trials where conditions were comparable to those of Tomasello *et al.* 1998).

Trial type	**(a) All**		**(b) Communicator produces visible behaviour while within targets' open or peripheral field of vision & targets are required to only turn around to look to the stimulus**	
	% reorientation	**N**	**% reorientation**	**N**
Towards	60.00	10	75.00	8
Away	40.00	10	100.00	1
All	50.00	20	77.78	9

Comparisons within conditions (of pre-stimulus and stimulus phases / 'Pre vs. post' control)

Targets were significantly more likely to look to the stimulus area during the stimulus than pre-stimulus phase of experimental trials (GLMM with 'phase' and 'look/no look' variables entered as factors, and participant as a random factor; All trials received: Estimate = 1.93, SE = 0.69, z = 2.79, $p = 0.005$). When the conditions where the target faced *towards* and *away* from the communicator at the start of the stimulus phase were analysed separately, targets were more likely to look to the stimulus area during the stimulus phase of trials where they faced *towards* but not *away* from the communicator ('*Experimental-Towards*': All trials received, GLMM: Est. = 1.91, SE = 0.90, z = 2.12, $p = 0.034$; Analysis of first trial received, McNemar test: $\chi^2 = 4.05$, N = 10, $p = 0.044$; *Experimental-Away:* All trials received, GLMM: Est. = 7.59, SE = 6.94, z = 1.09, $p = 0.274$; Analysis of first trial, McNemar test: $\chi^2 = 0.45$, N = 10, $p = 0.502$). There was no significant difference between targets looking to the stimulus when displayed outside the view of a '*Target Alone*' and '*Target and Ignorant Communicator*' (comparison of the stimulus phases of all trials of the two conditions: Fisher's Exact test: N = 57, $p = 0.55$). Therefore, and since '*Target Alone*' trials for some subjects were substituted by the more conservative '*Target and Ignorant Communicator*' trials, the two conditions were collapsed. There was no significant difference in the likelihood of targets looking to the stimulus area during the pre-stimulus and stimulus phases of any of the control trials ('*No Stimulus-Towards*': All trials received, GLMM: Est. = 0.00, SE = 190500[27], z = 0, $p = 1$, Analysis of first trial, McNemar test: $\chi^2 = 0.03$, N = 10, $p = 0.871$; '*No Stimulus-Away*': All trials received, GLMM: Est. = 0.00, SE = 1.77, z = 0.00, $p = 1$, Analysis of first trial, McNemar test: $\chi^2 = 0.03$, N = 10, $p = 0.871$; '*Target Alone*'/'*Target and Ignorant Communicator*': All trials received, GLMM: Est. = 0.00, SE = 0.85, z = 0, $p = 1$; Analysis of first trial, McNemar test: $\chi^2 = 0.08$, N = 10, $p = 0.779$, Figure 2.19).

Considering the duration of looks, targets overall oriented significantly longer (i.e., the stimulus fell within the targets' 'open' field of vision) towards the stimulus area during the stimulus phase (mean = 8.13s, s.d. = 5.55) than pre-stimulus phase of experimental trials (repeated measures t-test conducted on trials where targets oriented to the stimulus area during either the pre-stimulus or stimulus phase: mean = 4.88s, s.d. = 7.15, t(15) = -2.45, $p = 0.027$).

[27] The GLLM produces large standard errors in cases where only the value zero is entered into the model for a given factor. In the case of the '*No Stimulus-Towards*' condition targets looked to the stimulus location in zero cases of either the pre-stimulus nor stimulus phase.

Comparisons across conditions (of looks to the stimulus area during stimulus phases)

Targets were more likely to look to the stimulus area during the stimulus phase of *experimental* trials than control trials (All trial received, GLMM with 'look/no-look' and '*Experimental*', '*No Stimulus*' and '*Target Alone*'/'*Target and Ignorant Communicator*' conditions entered as factors, and participant as a random factor: '*Experimental*' vs. '*No Stimulus*': Est. = -3.12, SE = 1.07, z = 2.92, p = 0.004; *Experimental*' vs. '*Target Alone*'/'*Target and Ignorant Communicator*': Est. = -2.30, SE = 0.68, z = 3.50, p = 0.001, Figure 2.19, Table 2.5a).

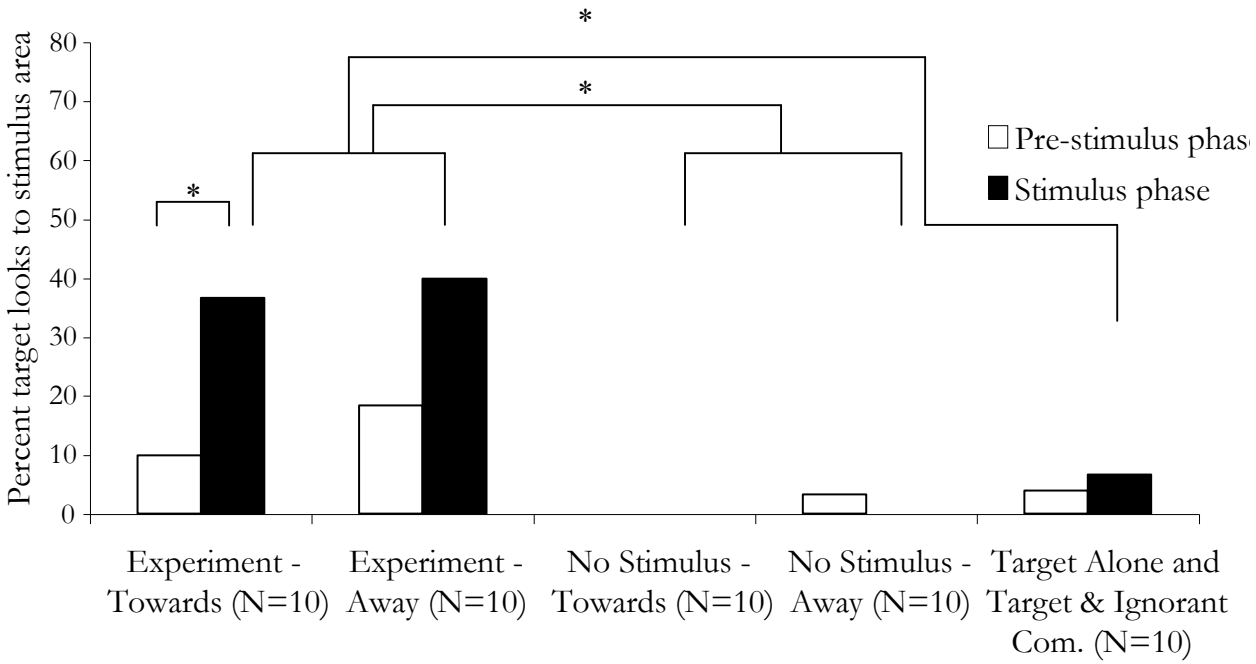


Figure 2.19: Target looks to the stimulus area. Percent target looks to the stimulus area during the pre-stimulus and stimulus phases of experimental and control conditions (percentages are based on the average response to the trials that individual subjects received). Asterisks indicate significant differences between target looks to the stimulus location during the pre-stimulus and stimulus phase of '*Experiment-Towards*' trials, and during the stimulus phases of *experimental* and control trials.

Trials requiring targets to only turn around to look to the stimulus

Considering only the subset of trials that required targets to turn around so a to look to the stimulus (i.e., no obstacle), targets were more likely to look to the stimulus area during the stimulus than the pre-stimulus phase of *experimental* trials (GLMM: Est. = 2.12, SE = 0.86, z = 2.48, p = 0.013). This result remained for trials, in which target animals faced *towards* (GLMM:

Est. = 2.57, SE = 1.17, z = 2.20, p = 0.028; Analysis of first trial, McNemar test: χ^2 = 5.06, N = 9, p = 0.024), but not *away* from the communicator at the start of the stimulus projection when the two experimental conditions were considered separately (Est. = 15.25, SE = 60.74, z = 0.25, p = 0.802; Analysis of first trial, McNemar test: χ^2 = 0.75, N = 6, p = 0.387). There were no significant differences between targets looking to the stimulus area during the pre-stimulus and stimulus phases of controls trials that required targets to only turn around ('*No Stimulus–Towards*': GLMM: Estimate = 0.00, SE = 130000, z = 0, p = 1; Analysis of first trial, McNemar test: χ^2 = 0.03, N = 7, p = 0.871; '*No Stimulus–Away*: Est. = 0.00, SE = 1.78, z = 0, p = 1; Analysis of first trial: χ^2 = 0.07, N = 7, p = 0.789; '*Target Alone*'/'*Target and Ignorant Communicator*': Est. = 0.00, SE = 0.84, z = 0, p = 1; Analysis of first trial: χ^2 = 0.05, N = 10, p = 0.823).

Targets were more likely to look to the stimulus area during the stimulus phase of *experimental* than control conditions ('*Experimental*' vs. '*No Stimulus*': GLMM: Est. = -3.15, SE = 1.10, z = 2.85, p = 0.004; '*Experimental*' vs. '*Target Alone*'/'*Target and Ignorant Communicator*': Est. = -2.61, SE = 0.73, z = 3.56, p = 0.000, Figure 2.20, Table 2.5b).

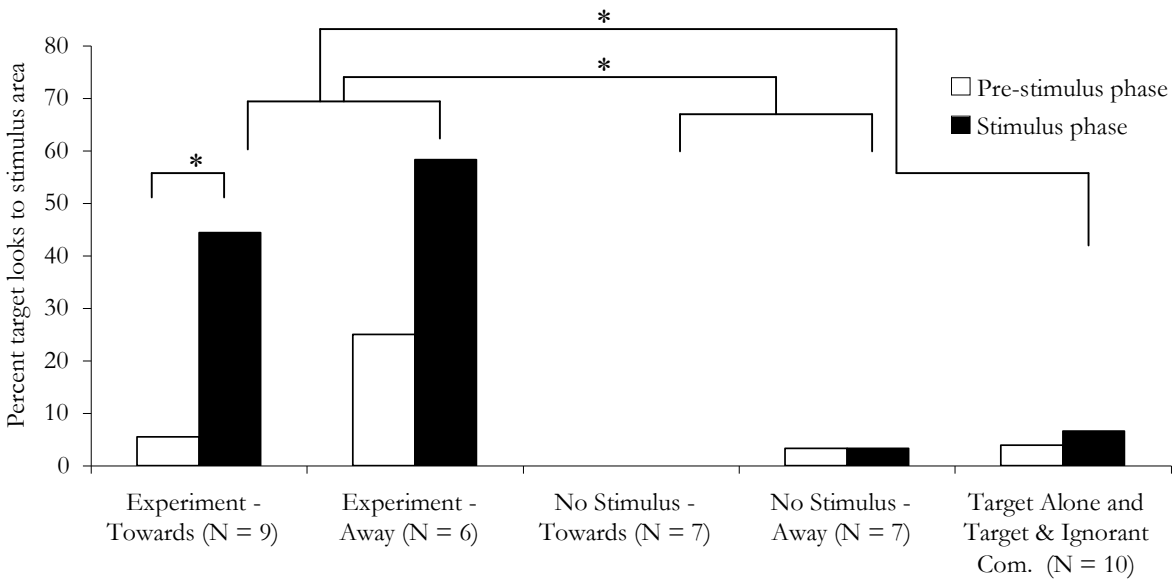


Figure 2.20: Turn trials. Percent target looks to the stimulus area during the pre-stimulus and stimulus phases of experimental and control trials that required targets to only 'turn' (measure is based on the average response to all 'turn' trials that individual subjects received). Since some subjects did not receive any 'turn' trials, N vary. Asterisks indicate significant differences.

Trials requiring targets to locomote around a visual barrier to look to the stimulus

Comparisons within conditions (of pre-stimulus and stimulus phases - '*Pre versus post*' control):

Considering only the subset of trials that required targets to first locomote around a visual barrier so as to look to the stimulus, there was no statistically significant difference between target looks to the stimulus area during the pre-stimulus and stimulus phase of neither *experimental* trials nor of any of the control trials ('*Experimental-Towards*', GLMM: Est. = 0.00, SE = 25.37, z = 0.00, p = 1; '*Experimental-Away*': Est. = -32.40, SE = 662006, z = 0.00, p = 1; *Experimental* trials analysed jointly: Est. = 1.71, SE = 1.25, z = 1.37, p = 0.172; '*No Stimulus–Towards*': Est. = 0.00, SE = 152700, z = 0, p = 1; '*No Stimulus–Away*': Est.= 0.00, SE = 1376600, z = 0, p = 1; '*Target Alone*'/'*Target and Ignorant Communicator*': Est. = 0.00, SE = 1376600, z = 0, p = 1; for analyses of first trials received [yielding non-significant differences across all conditions], see Table 2.5c).

Comparisons across conditions (of looks to the stimulus area during stimulus phases):

Comparing only trials that required targets to locomote around a barrier to look to the stimulus, there was no significant difference between targets looking to the stimulus area during the stimulus display phases of *Experimental* and control trials ('*No Stimulus*': GLMM: Est. = -18.56, SE = 5910, z = 0, p = 0.998; '*Target Alone*'/'*Target and Ignorant Communicator*': Est. = -18.56, SE = 7929, z = 0, p = 0.998, Figure 2.21, Table 2.5C).

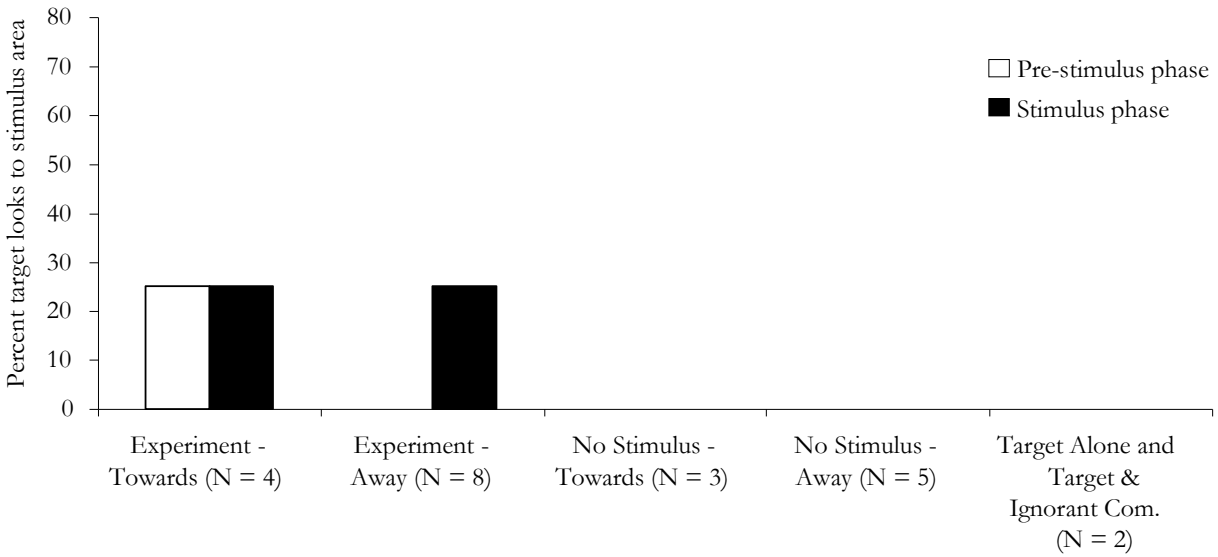


Figure 2.21: Locomote trials. Percent target looks to the stimulus area during the pre-stimulus and stimulus phases of experimental and control trials that required targets to first locomote around an obstacle (i.e., geometrical attention following trials; measure is based on the average response to all 'locomote' trials individuals subjects received).

Table 2.5: Results summary. Statistics for all trials (Table a), and for the data-subsets where targets were required to either only 'turn' (Table b), or to 'locomote' around a barrier to look to the stimulus (Table c). The hypotheses predicted a difference between target looks to the stimulus locations in comparisons 1-3 and 7-8, and none in comparisons 4-6. Significant differences are highlighted in grey.

a) All trials Trial type(s) compared	Intervals compared	GLMM				McNemar Test (first trial receive	
		Estimate	SE	z	*P*	χ^2	*P*
1 Experimental (all trials)	Pre- & Stimulus	1.93	0.69	2.79	0.005		
2 Exp. - Target faces towards com.	Pre- & Stimulus	1.91	0.90	2.12	0.034	4.05	0.044
3 Exp. - Target faces away from com.	Pre- & Stimulus	7.59	6.94	1.09	0.274	0.45	0.502
4 No Stimulus - Target faces towards com.	Pre- & Stimulus	0.00	190500	0.00	1.000	0.03	0.871
5 No Stimulus - Target faces away from com.	Pre- & Stimulus	0.00	1.77	0.00	1.000	0.03	0.871
6 Target Alone / Target & Ignorant com.	Pre- & Stimulus	0.00	0.85	0.00	1.000	0.08	0.779
7 Exp. & No Stimulus	Stimulus	-3.12	1.07	2.92	0.004		
8 Exp. & Target Alone/Target & Ign. com.	Stimulus	-2.30	0.68	3.50	0.001		

b) 'Turn' trials Trial type(s) compared	Intervals compared	GLMM				McNemar Test (first trial received	
		Estimate	SE	z	*P*	χ^2	*P*
1 Experimental (all trials)	Pre- & Stimulus	2.12	0.86	2.48	0.013		
2 Exp. - Target faces towards com.	Pre- & Stimulus	2.57	1.17	2.20	0.028	5.06	0.024
3 Exp. - Target faces away from com.	Pre- & Stimulus	15.25	60.74	0.25	0.802	0.75	0.387
4 No Stimulus - Target faces towards com.	Pre- & Stimulus	0.00	130000	0.00	1.000	0.03	0.871
5 No Stimulus - Target faces away from com.	Pre- & Stimulus	0.00	1.78	0.00	1.000	0.07	0.789
6 Target Alone / Target & Ignorant com.	Pre- & Stimulus	0.00	0.84	0.00	1.000	0.05	0.823
7 Exp. & No Stimulus	Stimulus	-3.15	1.10	2.85	0.004		
8 Exp. & Target Alone/Target & Ign. com.	Stimulus	-2.61	0.73	3.56	0.000		

c) 'Locomote' trials Trial type(s) compared	Intervals compared	GLMM				McNemar Test (first trial receive	
		Estimate	SE	z	*P*	χ^2	*P*
1 Experimental (all trials)	Pre- & Stimulus	1.71	1.25	1.37	0.172		
2 Exp. - Target faces towards com.	Pre- & Stimulus	0.00	25.37	0.00	1.000	0.13	0.724
3 Exp. - Target faces away from com.	Pre- & Stimulus	-32.40	662006	0.00	1.000	0.45	0.450
4 No Stimulus - Target faces towards com.	Pre- & Stimulus	0.00	152700	0.00	1.000	0.03	0.871
5 No Stimulus - Target faces away from com.	Pre- & Stimulus	0.00	136600	0.00	1.000	0.03	0.871
6 Target Alone / Target & Ignorant com.	Pre- & Stimulus	0.00	136600	0.00	1.000	2.50	0.617
7 Exp. & No Stimulus	Stimulus	-18.56	5910	0.00	0.998		
8 Exp. & Target Alone/Target & Ign. com.	Stimulus	-18.56	7929	0.00	0.998		

Inter-animal distance

Given the possibility of increased conspicuousness of communicator cues at high inter-animal proximity, the effect of proximity on attention following was examined. There was no significant difference in inter-animal distance at the start of the stimulus phase of experimental trials where targets looked (mean rank = 20.56) and did not look (mean rank = 17.53) to the stimulus area (Mann-Whitney *U* test: $U = 143$, $N_1 = 18$, $N_2 = 19$, $p = 0.408$), nor was there a difference between the smallest inter-animal distance during the stimulus phase of experimental trials where targets looked (mean rank = 18.75) and did not look (mean rank = 19.24) to the stimulus area ($U = 166.50$, $N_1 = 18$, $N_2 = 19$, $p = 0.893$).

2.2.4 Discussion

Chimpanzees followed conspecific attention when they faced another viewing a novel visual stimulus. This corroborates findings by Tomasello and colleagues (Tomasello *et al.* 1998). These authors, however, considered only trials, in which a primate communicator provided a "visible cue", such as raising its head at an 80º angle towards a presented food item, and excluded trials, in which communicators ignored the stimulus. In contrast, the present study included analysis of all received trials. If criteria similar to those used by Tomasello and colleagues were applied, and only trials where the communicator produced a visible cue were included, chimpanzees followed the attention of conspecifics in 78% of trials, comparable to the 80% found by Tomasello and colleagues (Tomasello *et al.* 1998). In contrast, when trials where the communicator did not produce a visible cue were included in the analysis, the percentage of gaze following (60%) was somewhat higher than that found by Pitman & Shumaker (35% chimpanzee conspecific gaze following) who applied a similar criteria. Chimpanzees in the present experiment, however, frequently produced behavioural cues to their attention, other than head and gaze direction. The effect of cues associated with detection of a novel stimulus are examined in the next chapter.

Naïve targets were more likely to orient towards the stimulus area when in the presence of a conspecific who viewed the stimulus, than in the control conditions, i.e., in the absence of a communicator or in the presence of a communicator ignorant as to the presence of the stimulus ('*Target Alone*'/'*Target and Ignorant Communicator*' control), and in the absence of the stimulus, while orienting either towards or away from a communicator ('*No Stimulus*' controls). A further

control (*'pre versus post'* control) compared targets' looks to the stimulus location during the 30s that the stimulus was shown, and the preceding 30s when it was not. In this case, targets were more likely to look to the stimulus area during the stimulus phase than pre-stimulus phase, when they faced *towards*, although not *away* from the communicator when the stimulus was initially shown. The lack of statistical significance (despite showing the right tendency) did not reflect a low frequency of targets looking to the stimulus area, but that targets also frequently, by chance, looked to the stimulus area during the pre-stimulus phase (i.e., often, turned around an looked to the communicator, and thereby, by consequence, the stimulus located in front of the communicator). While this raises the possibility that looks to the stimulus area during the stimulus phase resulted from chance rather than attention following, several points (see below) suggest attention re-orientation in response to conspecifics' behaviour.

In addition to testing for *direct* attention following, the experiment tested the hypothesis that experimentally naïve chimpanzees are able and inclined to follow the attention of conspecifics geometrically, in a non-competitive context. These analyses were performed post-hoc, and the proportions of trials requiring targets to either turn around or first locomote around a barrier to look to the stimulus therefore varied. There were, for example, 14 experimental trials, in which the target faced *towards* the communicator and was required to only turn around to look to the stimulus area (*turn* trials), while only 4 trials required the target to first locomote around a visual barrier to look to the stimulus area (*locomote* trials). While targets followed conspecific attention when they needed only turn around to look to the stimulus, there was no evidence of geometrical attention following, though the sample size, on which these analyses were based, was too small to produce meaningful results. Moreover, previous studies have demonstrated that chimpanzees are capable of taking conspecifics' visual perspective, geometrically in competitive food-related contexts (Hare *et al.* 2000, 2001).

The stimulus was removed immediately before it area fell within the targets' peripheral field of vision. While it remains a possibility that targets may have detected a flicker of the stimulus light immediately prior to its removal, accidental detection due to experimenter error was identified in two only trials, which were abandoned and excluded from the analysis. Targets oriented longer towards the stimulus area during the stimulus than pre-stimulus phase of experimental trials, suggesting an expectation of a point of interest. Thus, although the control measure comparing targets' look to the stimulus area during experimental trials where the target initially faced *away* from the 'communicator failed to reach significance (yet showed the right tendency), a seeming expectation of a point of interest and targets' performance in other control

trials suggest that, overall, chimpanzees re-orientated in response to a conspecific attention to the stimulus.

A significant limitation of the study was that subject dyads were not pre-selected, but chosen opportunistically. While dyad pre-selection, involving permutations of a subordinate communicator and dominant target, and *vice versa*, is preferable for a comparison of e.g., the effect of rank relationships on attention following, this was unfeasible due to the rarity of favourable experimental constellations and the preferred interactions and locations of the animals.

2.3 Study 2: Infant chimpanzees

2.3.1 Introduction

The visual interaction between primate mothers and infants has received much attention in developmental psychology. Chimpanzees pay attention to others' eyes and gaze direction shortly after birth, show neonatal facial imitation within one month of birth (Myowa-Yamakoshi *et al.* 2004) and engage in mutual gaze during the first 3 months of life (Plooij 1984; Bard *et al.* 2005; Okamoto-Barth & Tomonaga 2006). Chimpanzees tested below the age of 13 (Okamoto-Barth & Tomonaga 2006) and 36 months (Tomasello & Carpenter 2005) follow human gaze and pointing cues to one of several objects placed in front of them. By 20 months one infant studied longitudinally (without explicit differential reinforcement) followed experimenter-pointing cues to a target located next to its mother, behind the infant's back (Okamoto-Barth & Tomonaga 2006). In contrast, infants below the age of 36 months do not use head-turn cues when an experimenter looks to a point at the ceiling outside the infants' visual field (Tomasello *et al.* 2001). While not explicitly tested, this suggests that, although infants may co-orient to locations outside their own visual field where potentially interesting events might occur (given e.g., conspecific presence), they do not readily follow gaze cues to locations where no events are expected to occur. As humans, mother-infant chimpanzee dyads compensate decreased proximity and loss of physical contact with an increase in visual contact, and mutual gaze varies across chimpanzees groups as a function of physical contact (Okamoto-Barth *et al.* 2007b; Leavens 2009). While mutual gaze (synchronous looking) and non-synchronous looking may reduce the discomfort caused by increased distance between individuals (Okamoto-Barth *et al.* 2007b), it may also increase in ambiguous situations to simply reduce stress and discomfort.

When exposed to a novel object human-reared chimpanzees look referentially to their caregivers and adjust their behaviour according to the valence of the message they receive (Russell *et al.* 1997). Such social referencing is, however, more about disambiguating the significance of situations or objects, than about the sender and recipient, and it has been suggested individuals may apply the message they receive to only the object, without understanding the other's mental connection to the object (Egyed *et al.* 2004, cited by Liszkowski 2005). Twelve to twenty-four months old chimpanzees produce intentionally communicative gestures (C. Hobaiter, *pers. Com.*), yet engage in few triadic interactions around objects and third entities (Bard & Vauclair 1984; Tomonaga *et al.* 2004). While apes do engage in triadic interactions with conspecifics (e.g., beg for food and incorporate objects in collaborative play: e.g., Tanner & Byrne 2010), and even more so when interacting with human experimenters, systematic observations of mother-infant interactions (Bard & Vauclair 1984; Tomonaga *et al.* 2004) and experiments involving human experimenters (Tomasello & Carpenter 2005) reveal little communication about third entities and none that express a declarative or informative motive. Little is known about infant-to-infant attention following and no previous experiments have exposed infants to novel/interesting objects to test if they may bring about conspecific visual co-orientation through intentional or adventitious behaviours. This study followed the rationale and general method of the study involving adult chimpanzees, and tested if infant chimpanzees presented with a novel visual stimulus would bring about conspecific co-orientation.

2.3.2 Methods

2.3.2.1 Participants

Participants were three infant female chimpanzees between 20 and 31 months of age (Table 2.6), housed in a social group with 8 adult chimpanzees at Copenhagen Zoo.

Table 2.6: Infant chimpanzee communicators.

Individual	Sex	Date of birth	Age at time of experiment (months)	Father	Mother
Malou	Female	29.09.03	20-22	Carl	Mati
Semliki	Female	07.01.03	26-31	Carl	Cindy
Vega	Female	07.03.03	26-28	Carl	Olga

2.3.2.2 Design and Procedure

The experiment used the same general methods as the study with adult chimpanzees, although some conditions were excluded. Due to close proximity to and near-continual attention from mothers it was unfeasible to conduct the '*Communicator Alone*' and '*Target Alone'* controls, which required infants to be alone in the experimental enclosures. All participants received two trial sequences consisting of one '*Experimental-Towards'* trial, one '*Experimental-Away'* trial, one '*No Stimulus-Towards'* trial and two '*Target and Ignorant Communicator*' trials presented in a randomised order (Table 2.7). As mothers paid close attention to their infants, few occasions transpired, in which mothers faced away from their infants. All participants therefore received two additional '*Experimental-Towards'* trials (Table 2.6).

Table 2.7: Number and types of trials where infants served as communicators (*Experimental* and *'No stimulus'* trials) and targets (*Target and ignorant communicator'* trials).

Individual	Experimental		No Stimulus	Target & Ignorant
	Towards	Away	Towards	Communicator
Malou	4	2	2	4
Semliki	4	2	2	4
Vega	4	2	2	4

2.3.3 Results

Targets followed the attention of infants who viewed the stimulus in 83.33% (N = 12) and 50% (N = 6) of trials when they faced *towards* and *away* from the infant, respectively.

Comparisons within conditions (of pre-stimulus and stimulus phases - '*Pre versus post*' control):

Targets were more likely to look to the stimulus location during the stimulus phase than pre-stimulus phase of *experimental* trials (GLMM: Estimate = 2.56, SE = 0.82, z = 3.12, p = 0.002). This effect remained when the condition, in which the target faced *towards* the infant communicator at the start of stimulus projection, was considered separately, but not when the target faces away from the communicator (GLMM, '*Experimental-Towards*': Est. = 5.21, SE = 1.68, z = 3.01, p = 0.002; '*Experimental-Away*': Est. = 0.89, SE = 1.28, z = 0.70, p = 0.486, Table 2.8). There were no significant differences between targets looking to the stimulus area during the pre-stimulus and stimulus phases of any of the control trials ('*Target and Ignorant Communicator*': Est. = 0.79, SE = 1.32, z = 0.60, p = 0.632; '*No Stimulus-Towards*': Est. = 0.49, SE = 1.53, z = 0.53, p = 0.466, Figure 2.22).

Table 2.8: Trial and target types and results. The number of *experimental* trials that infants received, and trials in which targets (adult female, alpha male, peer) looked to the stimulus area.

Trial Type	Target								
	Adult Female			Alpha Male			Peer		
	N	Look	No Look	N	Look	No Look	N	Look	No Look
Towards	9	8	1	1	0	1	2	2	0
Away	5	2	3	0	0	0	1	1	0

Comparisons across conditions (of looks to the stimulus area during stimulus phases)

Targets were more likely to look to the stimulus area during the stimulus phase of *experimental* than '*Target and Ignorant Communicator*' trials (GLMM: Est. = 2.56, SE = 0.82, z = 3.11, p = 0.002), however, the difference between target looks to the stimulus area during the stimulus phase of *experimental* and '*No Stimulus*' control trials was non-significant, although it approached significance (GLMM: Est. = 2.26, SE = 0.93, z = 1.86, p = 0.064).

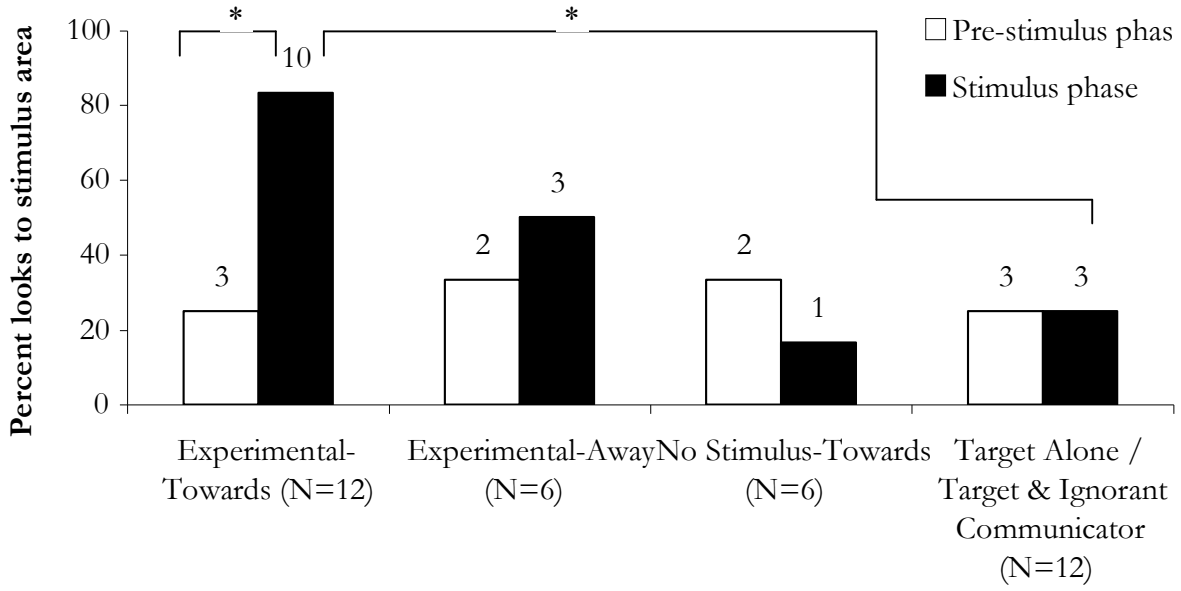


Figure 2.22: Target looks to stimulus area. Percentage of trials, in which targets looked to the stimulus area during the pre-stimulus and stimulus phases of experimental and control conditions. Asterisks indicates a significant differences between conditions.

Inter-animal distance

Given the possibility of increased conspicuousness of communicator cues at high inter-animal proximity, the effect of proximity on attention following was examined. There was no significant difference in communicator and target distance at the start of the stimulus phase of experimental trials where targets looked (mean rank = 9.23) and did not look (mean rank = 10.20) to the stimulus area (Mann-Whitney *U* test based on all received trials: $U = 29$, $N_1 = 13$, $N_2 = 5$, $p = 0.775$). Nor was there a difference between the *smallest* inter-animal distance during the stimulus phase of experimental trials where targets looked (mean rank = 9.65) and did not look (mean rank = 9.10) to the stimulus area ($U = 30.50$, $N_1 = 13$, $N_2 = 5$, $p = 0.849$). A similar pattern emerged when only trials, in which targets were the infant communicators' mother (inter-animal distance at the beginning of experimental trials: $U_{(4,8)} = 2.75$, NS; inter-animal distance at the closest point during experimental trials: $U_{(4,8)} = 2.88$, NS).

2.3.4 Discussion

Chimpanzees followed the attention of infants who viewed a novel stimulus in 83% of the trials when they faced *towards* the infant and in 50% when they faced *away* from the infant. They were more likely to look to the stimulus area when in the presence of an infant viewing the stimulus than in the control conditions, i.e., in the presence of an infant ignorant as to the stimulus ('*Target and Ignorant Communicator*'), and in the absence of the stimulus, while orienting towards the infant communicator ('*No Stimulus*'). Moreover, targets were also more likely to orient towards the stimulus display area during the 30s that the stimulus was presented, than the preceding 30s when it was not when the target initially faced *towards* though not *away* from the infant communicator. Conclusions regarding the latter should, however, be treated with caution, given the small number of trials of this type (two observations for each of three subjects). There was no difference in the distance between targets and communicators in experimental trials where targets looked/did not look to the stimulus area; neither when all trials and only trials in which the target was the communicator's mother were considered independently. This suggests that conspecific attention following was not a function of mother-infant proximity, and that adult females were no more likely to look and co-orient to infant's focus of attention when they were further away. Unfortunately, few trials (n = 3) involved infants as both communicators targets, however, the rare occasion of two infants found alone in an enclosure (without their mothers) limited the opportunity to conduct infant-to-infant attention following trials. Nonetheless, infant targets co-oriented to the attention of infant communicators in all three trials. Overall, the results suggest that infant chimpanzees consistently bring about conspecific co-orientation when presented with a novel/interesting visual stimulus.

2.4 Adult versus infant communicators

2.4.1 Introduction

The chimpanzees' performance in the experimental conditions of study 1 and 2 were compared to (1) test for differences in visual co-orientation to infant and adult communicators, and (2) explore whether any such difference might be influenced by variance in the inter-animal distance of mothers-infant and adult dyads, as a predicted higher proximity of mother-infant dyads, might make the infants' behaviours more conspicuous, and consequently account for a higher percentage of co-orientation to infant communicators.

2.4.2 Results and discussion

Targets looked to the stimulus area during the stimulus phase of experimental trials in 44.44% (8 of 18) and 83.33% (10 of 12) trials when they faced towards an adult and infant communicator viewing the stimulus, respectively, and in 31.58 (6 of 19) and 50% (3 of 6) of trials when they faced *away* from an adult and infant communicator, respectively (percentages based on all trials that the two subject categories received). There was, however, no significant effect of communicator category (infant/adult) on target looks to the stimulus area, when analysed by means of logistic regression, taking into account the repeated measures (GLMM: Est. = 0.71, SE = 2.86, z = 0.02, $p = 0.999$), most likely because of the very small sample size (N = 3) of infant communicators.

There was no overall difference in inter-animal distance at the start of the stimulus phase of experimental trials involving infant and adult communicators (Mann-Whitney *U* test: $U = 316.50$, $N_1 = 18$, $N_2 = 37$, $p = 0.766$), nor of experimental trials where targets looked ($U = 273.50$, $N_1 = 13$, $N_2 = 18$, $p = 891$) and did not look ($U = 41.50$, $N_1 = 5$, $N_2 = 19$, $p = 0.679$) to the stimulus area. The inter-animal distance at the closest point during the stimulus phase of experimental trials was smaller in trials involving infant (mean rank = 21.28, median distance = 62.50 cm) than adult communicators (mean rank = 31.27, median distance = 150 cm; $U = 212$, $N_1 = 18$, $N_2 = 37$, $p = 0.029$). Considering only trials where targets *looked* to the stimulus, there was, however, no significant difference in the inter-animal distance between those involving infant (mean rank = 13.31, median distance = 75.00 cm) and adult communicators (mean rank=17.94, median distance = 175.00 cm; U = 82.00 $n_1 = 13$, $n_2 = 18$, $p = 0.164$).

2.5 General Discussion

Overall, chimpanzees followed the attention of both adults and infants who viewed a novel stimulus. While previous research has demonstrated that chimpanzee conspecific attention following may occur under rather extreme circumstances, such as when a conspecific is induced to raise its head to an 80° upwards angle, and during more subtle interactions between humans and chimpanzees with much experimental experience (Povinelli & Eddy 1994, 1996b, 1997; Tomasello *et al.* 1998, 1999; Bräuer *et al.* 2005) the present experiment shows that co-orientation also occurs in interactions between experimentally naive animals to points that require only a small reorientation on the part of the communicator.

The experimental design did not require target animals to re-orient to points where interesting events (e.g., human or conspecific presence, see Tomasello *et al.* 1998; Okamoto-Barth & Tomonaga 2006; Pitman & Shumaker 2009) frequently occurred (but to walls or the ground upon which the stimulus was projected), which might be expected to otherwise increase readiness to co-orient on the basis of observed adventitious cues. For example, while Okamoto-Barth & Tomonaga (2006) found that one infant chimpanzee followed human gaze and pointing cues to a target located next to its mother, behind the infant's back, Tomasello and colleagues (Tomasello *et al.* 2001) found no evidence that infant chimpanzees follow human gaze cues to a point on the ceiling outside the infants' visual field (i.e., to a point without human/conspecific presence). Study 2 (infants) involved only three trials where infants served as (both communicators and) targets, and the results regarding infant attention following are therefore treated with caution. Infant targets, however, co-oriented to communicator attention in all trials, suggesting that infants (as adults) readily follow conspecific attentional cues to locations behind themselves where no events were expected to occur.

Although the stimulus was removed immediately before detected, targets in trials involving adult communicators oriented longer towards the stimulus area during the stimulus than pre-stimulus phase of experimental trials, suggesting an expectation of a point of interest.[28] While one control measure (comparison of targets' looks to the stimulus area during the pre-stimulus and stimulus phases of experimental trials where targets faced *away* from the communicator at the start of stimulus projection) failed to reach significance (yet showed the right tendency) a seeming expectation of a point of interest, and targets' performance in all

[28] The orientation of some targets (facing away from the video camera) in trials involving infant communicators did not allow for unambiguous coding of the duration of looks to the stimulus area, which was therefore not analysed for infant-communicator study.

other comparisons and control conditions suggest that, overall, chimpanzees re-orientated in response to conspecific attention to the stimulus.

The results match those found by Tomasello and colleagues (Tomasello *et al.* 1998), who compared the likelihood of several species, including chimpanzees, to detect food presented by an experimenter in an observation tower, while alone (with their back to the experimenter, equivalent to the '*Target Alone*' control used in the present design), or in the presence of conspecifics viewing the experimenter and food. Tomasello and colleagues did, however, not include the key baseline control ('*Target and Ignorant Communicator*' deployed in the present experiment) that examined the probability of targets detecting the stimulus by chance, when accompanied by a conspecific ignorant as to the stimulus. As this control was predicted to produce a slightly higher proportion of target chance looks to the stimulus area (as a result of increased scanning due to conspecific presence), the use by Tomasello and colleagues of a less conservative condition ('*Target Alone*') as their only control measure may (amongst other things) have contributed their design yielding significant effects. Tomasello and colleagues did also not examine target looks to the stimulus area while in the presence of a conspecific but absence of the stimulus (controlled in the present experiment by means of the '*No Stimulus*' control and '*Pre vs. Post*' control, comparing target looks to the stimulus area during and prior to the presentation of the stimulus). As the experimental pre-stimulus phase seemed to evoke somewhat higher proportions of looks to the stimulus location than both the pre-stimulus and stimulus phases of the control conditions, it is likely that pre-stimulus vs. stimulus phase control yields slightly different information, and thus represents a crucial measure for comparisons in gaze following paradigms. Finally, Tomasello and colleagues' inclusion of several individuals as communicators in any one trial (see Figure 1.1) precludes conclusions as to whether targets responded to the attention of one or several individuals; Viewing multiple individuals sharing a visual referent may reduce the threshold for initiation of automatic visual co-orientation. In contrast, the present experiment systematically controlled for possible alternative explanations by the inclusion of multiple control conditions and comparisons that overall suggest that chimpanzees re-orientated in response to conspecific attention to the stimulus, both when they faced *towards* and *away* form the communicator at the start of stimulus presentation.

While intra-specific geometrical gaze following has been implicitly demonstrated in competitive contexts (Hare *et al.* 2000; Hare *et al.* 2001), chimpanzees in the present experiment did not follow communicators' attention under unfavourable geometric conditions that required targets to locomote around a visual obstruction. The small sample size of '*locomote*' trials,

however, precludes conclusions regarding intra-specific geometrical gaze following.

Overall, the rate of following the attention of infant communicators was higher than that of adults, however, the comparison of conspecifics' responses to infant and adult communicators failed to yield a statistically significant difference, probably in part due to the very small number of infant communicators tested (N = 3). While the proximity of mother-infant dyads was higher at the closest point during experimental trials (though not at the beginning of trials), there was no difference in the proximity of mother-infant and adult dyads, respectively, in trials where targets followed and did not follow the communicators' attention to the stimulus area. Considering the comparatively higher proportion of attention following to infant communicators, this suggest that target conspecifics did not look to the stimulus presented to infant communicators as a function of proximity, but may pay closer attention and/or be more responsive to infants than adults, or alternatively, that the behaviours that infants produced upon viewing the stimulus were more conspicuous than those of adults (e.g., involved a higher degree of auditory or motion related behaviours). The next chapter will explore whether (and if so, which) behaviours produced by communicators consistently led to conspecific attention re-orientation, and if individuals intentionally redirected conspecifics attention.

CHAPTER 3: Chimpanzee manipulation of conspecific attention

Summary

Directing others' attention to distal locations is an adaptive skill that enables individuals to share and obtain useful information. This chapter aimed to identify possible behaviours that may act as cues triggering intra-specific attention following, and examined if the behaviour of 10 adult chimpanzees viewing a novel visual stimulus (see Chapter 2) differed as a function of conspecific presence and visual attention. Chimpanzees were more likely to produce stimulus directed behaviours when viewing the stimulus in the presence of a non-attending conspecific than alone, and conspecifics were more likely to look to the stimulus area when the communicator did so. There was a (non-significant but) clear trend for the chimpanzees to preferentially adopt a stimulus directional 'hunching' posture when viewing the stimulus in the presence of conspecifics, who were, in such cases, more likely to look to the stimulus area. Chimpanzees were more than twice as likely to produce an auditory behaviour in experimental trials where the conspecific faced away rather than towards them, and six times more likely to do so than when they viewed the stimulus on their own, although this difference was statistically non-significant. There was no species-wide evidence for active attention calling followed by directional behaviours, yet there were noticeable individual differences, with some chimpanzees consistently combining functionally different behaviours (an auditory component followed by a stimulus directed component) and consistently leading conspecifics' attention to the stimulus location. While the design did not eliminate the possibility of an interrogative social referencing motive underlying the attention directing ('look and help me decide how to respond'), the consistent production, by some animals, of sequential auditory-stimulus directional behaviours when viewing a novel stimulus in the presence of a non-attentive conspecific, is consistent with a declarative and social referential pointing interpretation. The results suggest that the paucity of observed pointing behaviours in chimpanzees may owe to the inconspicuousness and multi-faceted nature of the signals.

3.1 Introduction

There is an extensive number of examples of chimpanzees pointing in apparent requests for the delivery of food and other objects from humans, and considerable evidence that their pointing behaviours are referential and goal-directed (Leavens *et al.* 2005; for comprehensive reviews, see Leavens 2004; Leavens & Hopkins 1998)[29]. Savage-Rumbaugh (1986) reported 37 episodes involving pointing between two language (symbol)-trained chimpanzees (Sherman & Austin) in the context of a food-sharing task, where individuals frequently pointed to the food they wished the other to deliver. Although wild chimpanzees indicate parts of their own bodies (by means of exaggerated scratching behaviours) that conspecifics subsequently groom (Pika & Mitani 2006), pointing to distal objects has not been reported among wild populations, and without exception, the reported instances of chimpanzee pointing are subject to an imperative interpretation, i.e., they are about spurring others into action to do something for the subject. Apparent behaviours produced to elicit an attentional or emotional (and not necessarily immediately *behavioural*) reaction in conspecifics have been reported by Menzel (e.g., 1974) for chimpanzees covertly presented with various objects, that they later, actively, lead conspecifics to detect. Menzel suggested that chimpanzees may engage in postural and other forms of directional bodily deixis that may be inconspicuous, but meaningful to the animals. This suggestion has received much theoretical interest, but little empirical support.

This chapter aims to identify behaviours consistently produced by chimpanzees viewing a novel stimulus, which may act as cues triggering intra-specific attention following, and tests the hypothesis that chimpanzees have the ability and motivation to direct conspecifics to a novel, distal object and engage in signalling other than necessarily hand-pointing. To test if communicators actively called the attention of non-attentive conspecifics, and led them to look to a stimulus that only they observed, it was recorded whether communicators produced different behaviours or combinations thereof when: (1) in the presence of the stimulus but absence of a conspecific ('*Communicator Alone*'), (2) in the presence of the stimulus and an attentive or non-attentive conspecific (*Experimental* conditions, where the target faced *towards* or *away* from the communicator at the start of stimulus projection), (3) in the absence of the stimulus while in the presence of an either attentive or non-attentive conspecific ('*No Stimulus*' controls), and while in the presence of the stimulus, undetected by themselves, either alone or in

[29] As language trained birds (e.g., Pepperberg 2009), chimpanzees will also indicate the location of a named object, e.g., point to its nose when asked "show me your nose, where is your nose" (Kellogg & Kellogg 1933, cited by Leavens 2009).

the presence of a conspecific ('*Target Alone*' and '*Target and Ignorant Communicator*' controls). It was predicted that communicators would behave differently as a function of conspecific presence and visual attention. Specifically, it was predicted that there would be

(i) A difference in the frequency of auditory behaviours produced when in the presence of the stimulus and an attentive or non-attentive conspecific (*experimental* conditions).

(ii) A difference in the frequency of visual stimulus directional behaviours when in the presence of the stimulus and either presence (*experimental* conditions) or absence of a conspecific ('*Communicator Alone*' condition).

(iii) No difference in the frequency of other visual behaviours (arrest current behaviour, head bobbing etc.) in *experimental* and '*Communicator Alone*' conditions.

It was predicted that targets' looks to the stimulus area would be influenced by communicators' behaviour, and that there would be

(iv) A difference in the likelihood of non-attentive conspecifics looking to the stimulus area when communicators did or did not produce auditory behaviours.

(v) A difference in the likelihood of conspecifics looking to the stimulus area when communicators did or did not produce stimulus directional behaviours.

(vi) No difference in the likelihood of conspecifics looking to the stimulus area when communicators did or did not produce behaviours *not* directed towards the stimulus.

The chapter indirectly examined the suggestion that apes may use gaze as a communicative signal (de Waal 2001) by examining communicators' and targets' gaze behaviour. It was predicted that there would be:

(vii) A difference in the likelihood that a target conspecific looked to the stimulus area when - while within a target's 'open' or 'peripheral' field of vision - a communicator looked to the target within 2s of looking away from the stimulus, followed by a look to the stimulus within 2s of looking away from the target (communicator gaze sequence: stimulus-target-stimulus, while being within a target's 'open'/'peripheral field of vision). Due to the difficulty of distinguishing such behaviour from social referencing (where chimpanzees exposed to a novel object look referentially to their caregivers and adjust their behaviour according to the valence of the message they receive: Russell *et al.* 1997), only *experimental* trials, in which communicators also produced an auditory cue, were examined to test this

prediction. Thus, the hypothesis that chimpanzees might use gaze as a communicative behaviour would be supported if targets were more likely to look to the stimulus location when communicators produced an auditory behaviour, followed by stimulus-target-stimulus gaze behaviours while being within the targets 'open'/'peripheral' field of vision.

(viii) There would be a difference in the likelihood of conspecifics looking to the stimulus area when communicators produced the above behaviours.

3.2 Methods

3.2.1 Design and procedure

The analyses were based on the experiment described in Chapter 2, involving 10 adult chimpanzees. The key comparisons involved the '*Communicator Alone*' and *experimental* conditions, to test if behaviours produced by chimpanzees who viewed the stimulus while alone, or in the presence of an either attentive, or non-attentive conspecific, reflected a heightened state of arousal, or possessed a communicative function, i.e., if communicators took conspecific presence and attentional state into account. The conditions were presented in a predetermined order (see Figure 2.3), in which 50% of participants received a '*Communicator Alone*' trial before the first experimental trial (one participant, co-housed with a conspecific in one enclosure could, however, not be tested alone and did therefore not receive the '*Communicator Alone*' condition). A second coder coded 30% (11 of 37) of experimental and 53% (9 of 17) of '*Communicator Alone*' trials to assess inter-observer reliability in terms of (1) auditory cues, (2) stimulus directional cues and (3) 'hunching' behaviour (see below for definitions). Inter-observer reliability with respect to all cues was very good (Cohen's kappa = 0.80 n = 20)

3.2.2 Coding of Communicator Behaviour

The following communicator behaviours were coded: (1) auditory behaviours (vocalise, stamp or knock on the ground, clap, audibly move object), (2) visual non-stimulus directional behaviours (arrest current behaviour, bipedal swagger, shake arm or leg silently, bob head, move head back rapidly), (3) visual stimulus directional behaviours (touch, lean torso towards, move extremity or head in the direction of the stimulus), (4) locomotory stimulus directional behaviour (approach stimulus area), and (5) behaviour directed at conspecific (looks to the conspecific that were preceded within 2s of a look to the stimulus, and instances where communicators produced an auditory behaviour and subsequently shifted gaze from the stimulus to the conspecific and back to the stimulus, Table 3.1). Only trials, in which the communicator's gaze behaviour could be reliably coded were included. A stimulus directional 'hunching' posture' (see Table 3.1 for definition), observed during the second trial conducted, was scored (if it occurred) in all trials. Cues were analysed as part of a behavioural category, apart from conspecific directed behaviours and the 'hunching' posture, which were analysed individually. Communicator behaviour was recorded during the 30s stimulus phases, yet presence/absence of the cues 'swagger', 'shake extremity', 'shake object', 'bob head', 'head back', approach stimulus area' (cues f-j, p, Table 3.1) were scored as being present or absent during both the pre-stimulus and stimulus phases, and recorded if they occurred in stimulus phase only. Auditory cues were recorded by two camcorders (i.e., not a separate microphone).

3.3.3 Statistics

While the experiment used a repeated measures design, the conditions compared contained unequal numbers of observations[30]. The distribution of communicator behaviours across the conditions, and of targets' look to the stimulus area when communicators produced particular behaviours, were therefore analysed by means of repeated measures binomial logistic regressions (fitted by the Laplace approximation) with a binomial error structure. Communicator identity was included as a random factor in the GLMM to deal with the issue of potential pseudo-replication of repeated measures, and of unequal numbers of observations (and hence, unequal contribution to the dataset) for different subjects. Gaze behaviours were

[30] For example, for every non-social trial ('*Communicator Alone*') there were two social trials ('*Experimental-facing towards*', '*Experimental-facing away*'), and one participant co-housed with a conspecific could not receive the '*Communicator Alone*' control trial (see section 2.2.2.3 and 2.2.2.4 for further details regarding unequal number of trials across the conditions and analyses).

analysed by means of binomial tests. Null-hypotheses were rejected at an alpha level of 5%.

Table 3.1: Behaviour definitions and classes.

Behavioural Class	Behaviour	Definition
(1) Auditory	(a) Vocalise	Signaller vocalises
	(b) Stamp	Signaller stamps on the ground, repeatedly while shifting its weight from foot to foot
	(c) Knock	Signaller knocks on the ground
	(d) Move object	Signaller audibly moves object
(2) Visual non-stimulus directional	(e) Arrest behaviour	Signaller arrests current behaviour
	(f) Swagger	Signaller sways from side-to-side with shoulders hunched, hair bristling and arms held (slightly) out
	(g) Shake extremity	Signaller shakes hand or arm
	(h) Shake object	Signaller shakes object silently
	(i) Bob head	Signaller moves head rapidly up and down two or more times
	(j) Head back	Signaller moves head backwards and upwards rapidly
(3) Visual stimulus directional	(k) Touch	Signaller touches the stimulus with its hand or mouth
	(l) Lean	Signaller reorients so that its torso leans towards the stimulus or stands up on all four orienting towards the stimulus
	(m) Extend extremity	Signaller extends arm or hand towards the stimulus
	(n) Move head	Signaller pushes head forward towards stimulus
	(o) Hunch	A stimulus-directed action-based behaviour, in which the animal rounds its back, tilts its body towards the stimulus, so it is within 20 degrees to either side of the saggital plane between the animal's shoulders, draws its head into its shoulders and pushes its chin forward towards the stimulus.
(4) Locomotory stimulus directional	(p) Approach	Signaller approaches simulus area
(5) Conspecific directional	(q) Gaze 1	Signaller looks to conspecific within 2s of looking to the stimulus
	(r) Gaze 2	Signaller produces an auditory behaviour and looks to a conspecific within 2s of looking to the stimulus, followed by a look to the stimulus within 2s of looking away from the conspecific (gaze behaviour: stimulus-target-stimulus). Only trials scored unequivocallly are included.

3.3 Results

3.3.1 Communicator behaviour

Visual stimulus directional behaviours Chimpanzees produced stimulus directional behaviours (touch, lean torso, extend extremity or move head in the direction of the stimulus) in 48.65% (N = 37) of trials when viewing the stimulus in the presence of a conspecific compared to 17.65% (N = 17) when alone. Moreover, 60% (N = 10) of communicators produced stimulus directional behaviours during a larger proportion of social than non-social trials, and none during a larger proportion of non-social trials (Figure 3.2). Nonetheless, the likelihood of producing a stimulus directional behaviour when in presence of a conspecific only approached significance. (GLMM, the conditions entered as factors and participant as a random factor: Social: Est. = 1.17, SE = 0.68, z = 1.73, p = 0.084; Non-social: Ext.: -1.21, SE = 0.62, z = 0.13, p = 0.120). Stimulus directional behaviours were, however, non-randomly distributed across the three main conditions, and communicators were more likely than chance to produce a stimulus directional behaviour when viewing the stimulus in the presence of a non-attending conspecific, though not when in the presence of an attending conspecific, or when alone (GLMM: '*Experimental-Towards*': Est. = 0.74, SE = 0.77, z = 0.96, p = 0.336; '*Experimental-Away*': Est. = 1.58, SE = 0.76, z = 2.09, p = 0.037; '*Communicator Alone*': Est. = -1.21, SE = 0.64, z = 0.982, p = 0.155, Table 3.2).

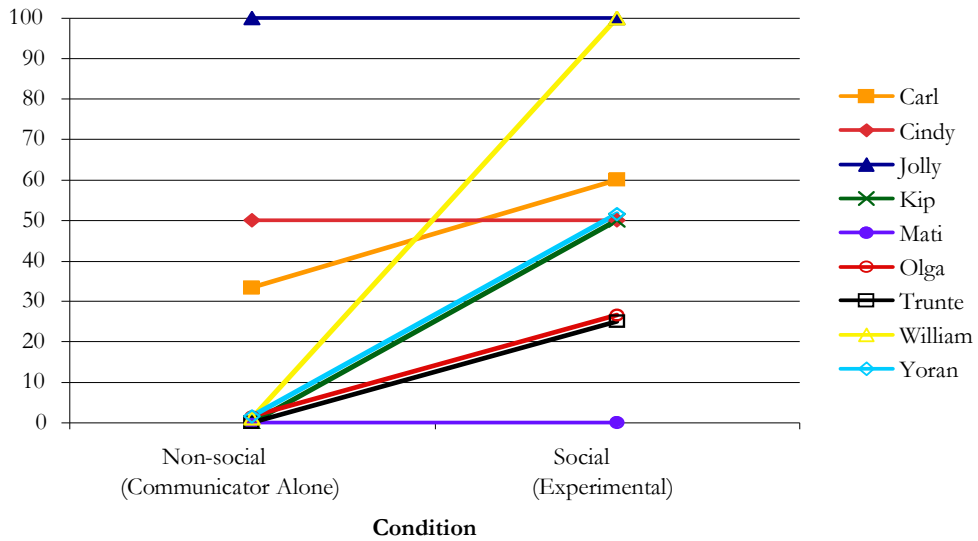


Figure 3.2: Production of stimulus directional behaviours by communicators in non-social ('*Communicator Alone*') and social (*experimental*) conditions.

'Hunching' stimulus directional behaviour: Chimpanzee communicators adopted a 'hunching' posture in 33.33% (12 of 37) of social (*experimental)* trials and in 5.88% (1 of 17) non-social trials ('*Communicator Alone*'). Nonetheless, the probability of 'hunching' occurring in social trials only approached significance, while it was non-significant for non-social trials (GLMM: Social: Est. = 2.92, SE = 1.53, z = 1.91, p = 0.056; Non-social: Est. = -2.56, SE = 1.69, z = 1.20, p = 0.700; Figures 3.3 and 3.4). When the three conditions were analysed individually, a similar picture emerged, with the production of 'hunching' approaching significance for the *experimental* conditions but not the '*Communicator Alone*' condition (GLMM with the three conditions entered as factors and participant as a random factor, '*Experimental-Towards*': Est. = 3.05, SE = 1.60, z = 1.90, p = 0.057; '*Experimental-Away*': Est. = 2.82, SE = 1.59, z = 1.78, p = 0.075; '*Communicator Alone*': Est. = -3.57, SE = 1.69, z = 0.70, p = 0.690). In all '*Experimental-Away*' trials where communicators adopted a 'hunching' posture (N = 6), 'hunching' was preceded by an auditory behaviour, while this was the case in only 33.33% (N = 6) of '*Experimental-Towards*' trials. Communicators did not adopt the 'hunching' posture in any of the '*No Stimulus*', '*Target Alone*'/'*Target and Ignorant Communicator*' control trials (N = 95).

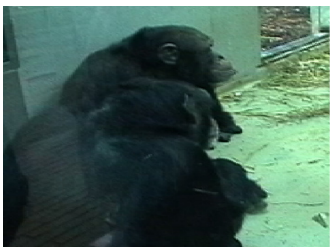
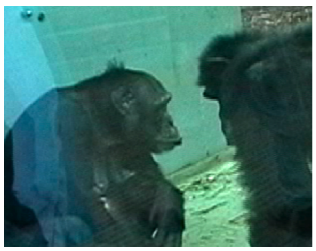
(a)  (b)  (c) 

Figure 3.3: 'Hunching' posture. Posture performed by the chimpanzees on the top left (still a), left (still b) and right (still c).

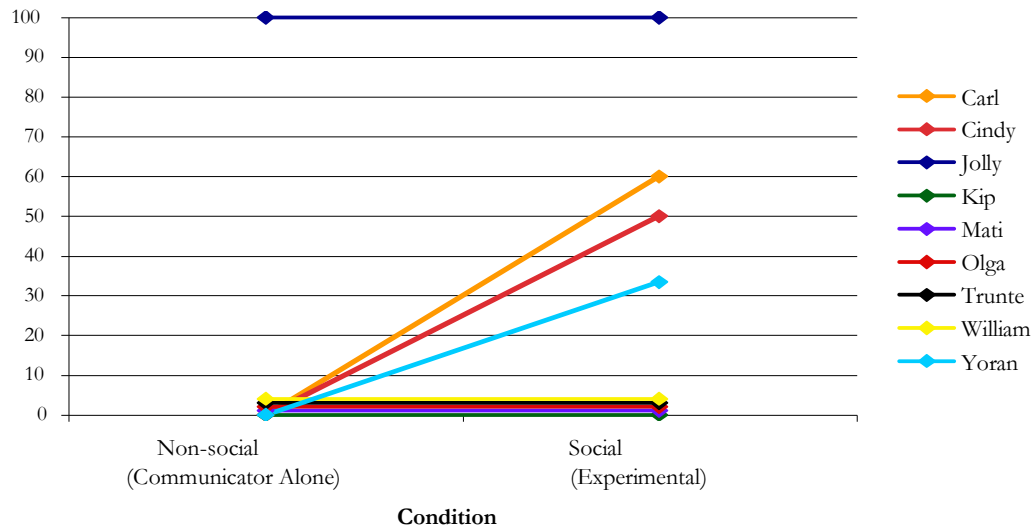


Figure 3.4: Adoption of 'hunching' posture in non-social ('*Communicator Alone*') and social (*experimental*) conditions (the chimpanzee Jolly received only one '*Communicator Alone*' trial).

Locomotory and visual non-stimulus directional behaviours: The distribution of locomotory (approach stimulus) and visual non-stimulus directional behaviours (arrest behaviour, bipedal swagger, shake arm or leg silently, bob head, move head back rapidly) across the three conditions did not deviate significantly from chance (see table 3.2).

Auditory behaviours: Chimpanzees produced an auditory behaviour (vocalisation, stamp, knock, clap, audibly move object) in 5.88% (N = 17), 16.67% (N = 18) and 36.84% (N = 19) of trials where they viewed the stimulus alone ('*Communicator Alone*'), or in the presence of an attentive ('*Experimental-Towards*') or non-attentive conspecific ('*Experimental-Away'*), respectively. The likelihood of communicators producing auditory behaviours in any of the conditions did, however, not deviate from chance, although it approached significance for the '*Experimental-Away*' condition (GLMM: '*Experimental-Towards*': Est. = 0.24, SE = 1.39, z = 0.17, p = 0.860, '*Experimental-Away*': Est. = 2.29, SE = 1.29, z = 1.75, p = 0.079; '*Communicator Alone*': Est. = -1.21 SE = 0.63, z = 1.20, p = 0.099). Moreover, while comparison of the social (*experimental*) and non-social ('*Communicator Alone*') conditions, also failed to yield significant effects (Social: Est. = 1.36, SE = 1.11, z = 1.22, p = 0.222; Non-social: Est. = -3.38, SE = 1.34, z = 1.52, p = 0.116), 33% of chimpanzees produced auditory behaviours during a larger proportion of social than non-social trials, and none produced auditory behaviours during a larger proportion of non-social trials (Figure 3.1).

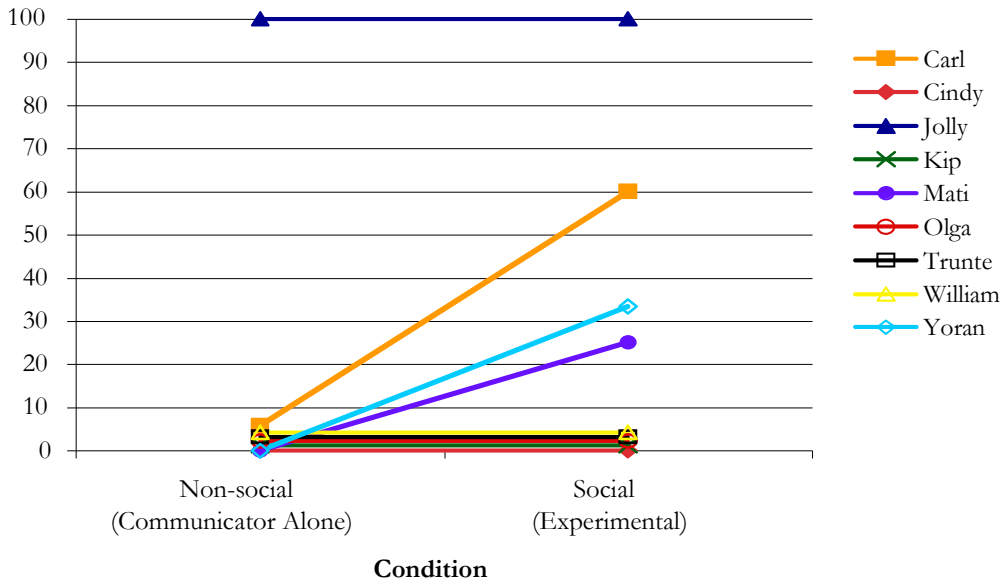


Figure 3.1: Production of auditory behaviours by communicators in non-social ('*Communicator Alone*') and social (*Experimental*, facing towards/away) conditions. One individual did not receive a '*Communicator Alone*' trial (as the individual was co-housed with another individual), and data are therefore presented for only 9 participants.

Multimodal behaviours: There was no significant difference in the production of multimodal behaviours, where an auditory behaviour preceded a visual stimulus directional behaviour, across the three conditions (GLMM: *'Experimental-Towards'*: Est. = -0.47, SE = 1.39, z = 0.34, p = 0.735, '*Experimental-Away*': Est. = 1.74, SE =1.25, z =1.39, p = 0.165; '*Communicator Alone*': Est. = -3.42, SE = 1.48, z = 0.28, p = 0.846, Figure 3.5). There were, however, noticeable individual differences. Two individuals (Carl and Jolly) preceded a directional behaviour by an auditory behaviour in all (n = 5) *experimental* trials where the target faced *away* from the communicator. Moreover, during '*Experimental-Away'* trials (and never during '*Experimental-Towards'* and '*Communicator Alone*' trials), the dominant male of one group (Carl) consistently (in 3 of 3 trials) produced an auditory behaviour (knocked on the ground) and subsequently hand-gestured and/or leaned in the direction of the stimulus, while repeatedly alternating gaze between the stimulus and conspecific. No auditory behaviours followed by directional visual behaviours were observed in control conditions where communicators did not view the stimulus ('*No stimulus'*, '*Target Alone'*/'*Target and Ignorant Communicator*', N = 95).

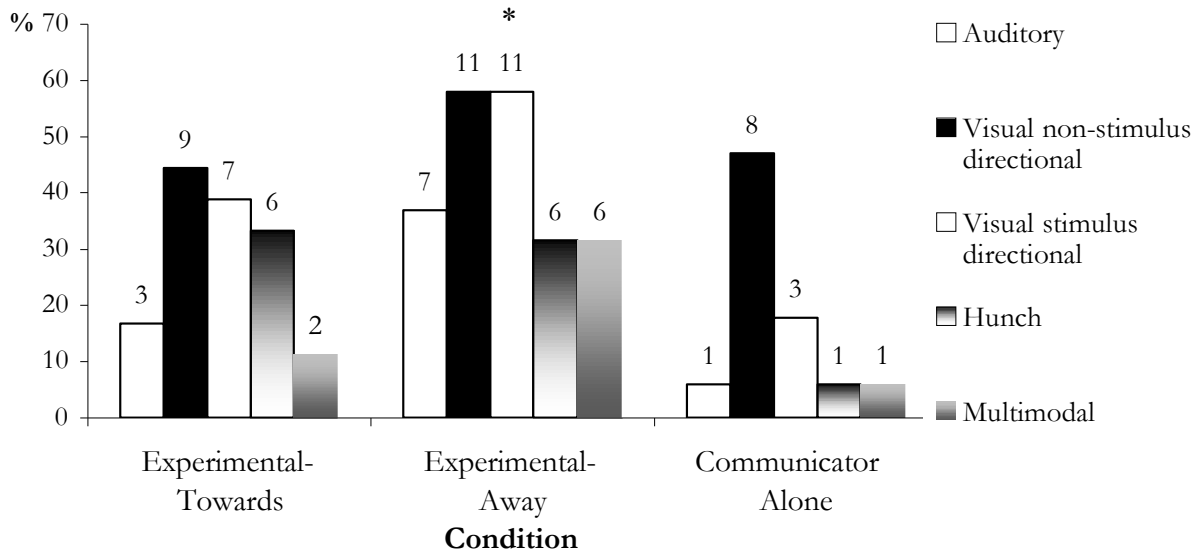


Figure 3.5: Communicator production of behaviours across conditions. Percentage of '*Experimental-Towards*' (N = 18), '*Experimental-Away*' (N = 19) and '*Communicator Alone'* (N = 17) trials, where communicators produced auditory, visual non-stimulus directional, visual stimulus directional and multimodal behaviours. Asterisk indicates significant differences across conditions.

Conspecific directional behaviours: Sixty-two percent (23 of 37) of *experimental* trials could be reliably scored for gaze changes. Of these, communicators were no more likely than chance to look to the target within 2s of looking away from the stimulus (60.68% (14 of 23) of trials, Binomial test: n = 23, p = 0.188). Communicators produced an auditory behaviour in 10 of 37 *experimental* trials, of which gaze behaviour could be reliably scored in eight trials. In 75% (6 of 8) of these trials communicators looked to the target conspecific within 2s of looking away from the stimulus, followed by a look to the stimulus within 2s of looking away from the conspecific (i.e., auditory behaviour followed by stimulus-target-stimulus gaze behaviour, while being within the conspecific's 'open'/'peripheral' field of vision). Communicators were no more likely than chance to perform this behaviour (Binomial test: n = 8, p = 0.289).

Table 3.2: Results summary for GLMM analyses of the distribution of communicator behaviours across the '*Communicator Alone*', '*Experimental-Away*' and '*Experimental-Towards*', and, separately, for social (*Experimental*) and non-social ('*Communicator Alone*') conditions. Significant and near-significant factors are highlighted in grey.

Behaviour	Model	Fixed effects	Estimate	Std. Error	z-value	P
Stimulus directional	1	Communciator Alone	-1.21	0.64	0.98	0.155
		Experimental-Away	1.58	0.76	2.09	0.037
		Experimental-Towards	0.74	0.77	0.96	0.336
	2	Non-social	-1.21	0.62	0.13	0.120
		Social	1.17	0.68	1.73	0.084
Locomotory directional	3	Communciator Alone	-2.18	1.27	1.51	0.121
		Experimental-Away	1.78	1.29	1.34	0.166
		Experimental-Towards	1.51	1.32	1.15	0.251
Non-stimulus directional	4	Communciator Alone	0.15	0.56	0.26	0.799
		Experimental-Away	0.45	0.69	0.65	0.517
		Experimental-Towards	0.15	0.70	0.22	0.830
Hunch	5	Communciator Alone	-3.57	1.69	0.70	0.690
		Experimental-Away	2.82	0.59	1.78	0.075
		Experimental-Towards	3.05	1.60	1.90	0.057
	6	Non-social	-2.56	1.69	1.20	0.700
		Social	2.92	1.53	1.91	0.056
Auditory	7	Communciator Alone	-1.21	0.63	1.20	0.099
		Experimental-Away	2.29	1.29	1.75	0.079
		Experimental-Towards	0.24	1.39	0.17	0.860
	8	Non-social	-3.38	1.34	1.52	0.116
		Social	1.36	1.11	1.22	0.222
Multimodal	9	Communciator Alone	-1.85	1.48	1.60	0.146
		Experimental-Away	1.74	1.25	1.39	0.165
		Experimental-Towards	-0.47	1.39	0.34	0.735

3.3.2 Communicator behaviours leading targets to look to the stimulus area

Conspecifics were significantly more likely to look to the stimulus area in *experimental* conditions when communicators produced (than did not produce) a stimulus directional behaviour (touch, lean torso, extend extremity or move head in direction of the stimulus), a multimodal behaviour, and adopted a 'hunching' posture, respectively (Table 3.3). There were only two experimental trials, in which 'hunching' occurred and did not lead targets to co-orient to the communicators' focus at the stimulus. In one of these, the stimulus was shown on one side of an artificial termite mount, and the target observed the communicator attentively (looked while arresting its behaviour), as the communicator slapped its hand on (another part of) the termite mount, and subsequently approached and began to groom the target. Communicators' production of locomotory stimulus directional, visual non-stimulus directional and auditory behaviours did not significantly affect conspecifics' looks to the stimulus area. The communicators production of gaze cues (Gaze 1: looked to the conspecific within 2s of looking away from the stimulus; $N_{\text{Gazec ue}} = 14$, $N_{\text{No Gazec ue}} = 11$; Gaze 2: followed an auditory behaviour with gaze shifts from the stimulus to the target and back to the stimulus, while being within the conspecific's 'open'/'peripheral' field of vision) also failed to yield a significant effect on whether or not targets looked to the stimulus area (Gaze 1: Est. = 1.74, SE =1.25, z = 0.89, p = 0.465; Gaze 2: Est. = 1.31, SE = 1.02, z = 0.97, p = 0.167). Figures 3.6 and 3.7 show targets looks to the stimulus area when communicators produced various behaviours.

Table 3.3: Significance table. GLMM tests (model 1-5) for a difference in the probability that targets looked to the stimulus area when communicators produced particular behaviours while viewing the stimulus during *experimental* trials. Significant and near-significant factors are highlighted in grey.

Model	Fixed effects	Estimate	Std. Error	z-value	*P*
1)	Intercept	-2.58	0.93	2.80	0.005
	Stimulus directional	3.11	1.14	2.73	0.006
	Locomotory stimulus directional	-1.26	1.41	0.89	0.373
	Auditory	1.81	1.53	1.18	0.237
	Non-stimulus directional	0.13	1.19	0.11	0.913
2)	Intercept	-1.66	0.55	3.04	0.002
	Hunch	3.27	0.95	3.45	0.001
3)	Intercept	-0.53	1.65	0.92	0.335
	Gaze 1 (gaze shifts)	0.15	1.21	0.10	0.938
4)	Intercept	-0.47	1.78	1.1	0.978
	Gaze 2 (auditory & gaze shifts)	0.85	1.76	0.32	0.642
5)	Intercept	-1.15	0.43	2.64	0.008
	Multimodal	3.09	1.15	2.68	0.007

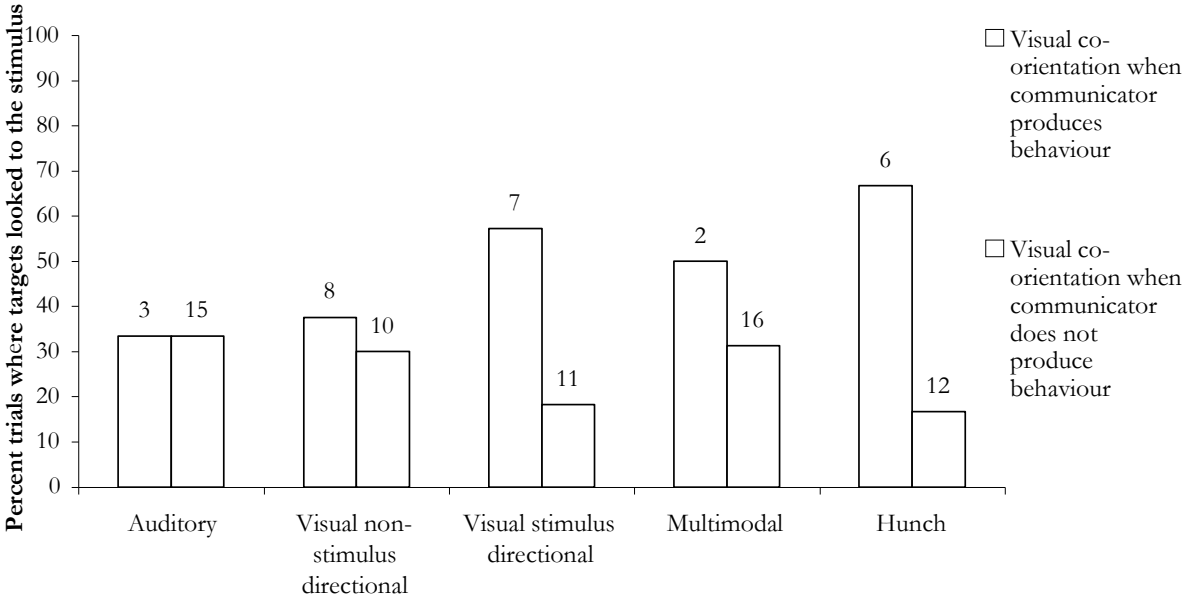


Figure 3.6: Attentive targets' looks to stimulus area as a function of communicator behaviour. Percentage of conspecific looks to the stimulus area during '*Experimental-Towards'* trials (N = 18) when communicators did/did not produce various behaviours (percentage based on all received trials). Labels above columns indicate the number of trials, in which communicators did/did not produce the behaviour.

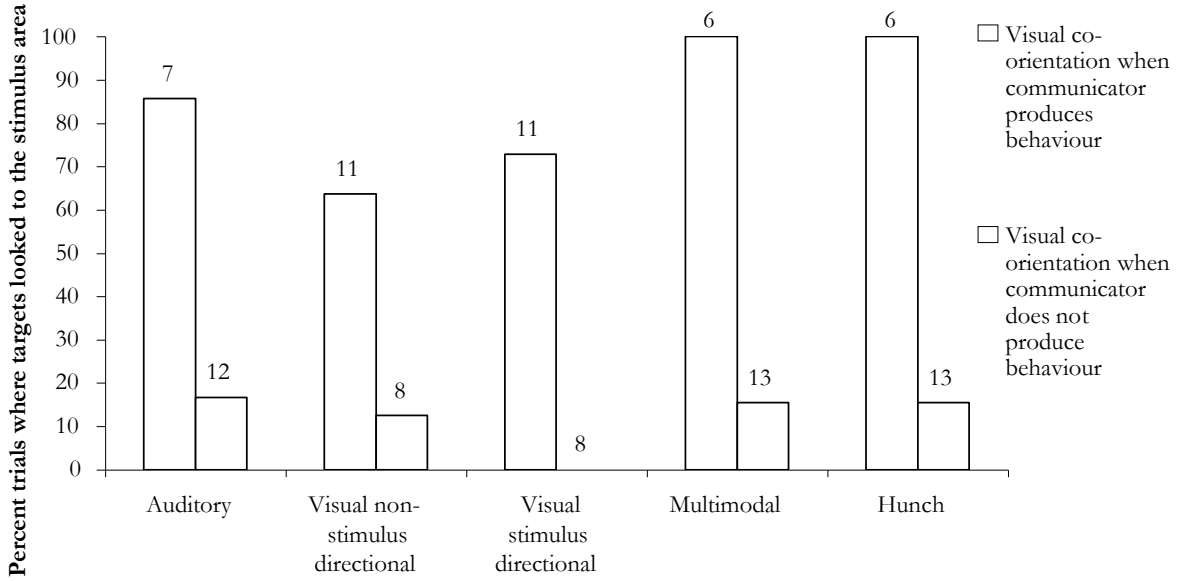


Figure 3.7: Non-attentive targets' looks to stimulus area as a function of communicator behaviours. Percentage of conspecific looks to the stimulus area during '*Experimental-Away'* trials (N = 19) when communicators did/did not produce various behaviours. Labels above columns indicate the number of trials, in which communicators did/did not produce the behaviour.

3.4 Discussion

This chapter aimed to identify behaviours that may act as cues triggering intra-specific attention following in chimpanzees, and test the hypothesis that chimpanzees have the ability and motivation to direct conspecifics to novel, distal objects, and engage in declarative-like signalling. Chimpanzees who viewed a novel laser stimulus were more likely to produce a directional behaviour (touch, lean torso, move extremity or head forward in the direction of the stimulus) when in the presence of an initially non-attending conspecific than when alone (or indeed in the presence of an *attending* conspecific). There was a non-significant, but nonetheless clear trend of the animals to preferentially produce a directional behaviour in conditions where they viewed the stimulus in the presence of a conspecific (attentive as non-attentive), rather than in a non-social context where they viewed the stimulus while alone. Moreover, conspecifics were more likely co-orient to the communicators' attention when communicators produced a directional behaviour. Overall, this suggests that, as a compound gesture, directional behaviours may carry a communicative function.

Chimpanzees adopted a 'hunching' posture (an action-based behaviour, in which the animal rounded its back, drew its head into its shoulders, leaned its body forward and pushed its chin towards the stimulus) in 33% (12 of 37) of trials where they viewed the stimulus in the presence of a conspecific and only once while alone. While the preferential adoption of the posture when viewing the stimulus in a social context failed to reach full significance (p = 0.056), a clear trend was evident. Moreover, in all cases where chimpanzees adopted the posture while viewing the stimulus in the presence of a *non*-attentive conspecific (N = 6), it was preceded by an auditory behaviour, while this was the case in only a third (N = 6) of cases where they viewed it in the presence of an attentive conspecific. Furthermore, conspecifics were more likely to look to the stimulus when communicators adopted the 'hunching' posture. The 'hunching' behaviour is similar to the 'quadrupedal hunch' described by Estes where the chimpanzee's "head is bent and drawn into the shoulders while the individual is in a quadrupedal stance, and the back is rounded" (Estes 1991, p. 554). Estes described the behaviour as a "high-intensity threat display to an opponent who is equal or near equal, and an attack may come after this" (Estes 1991, p 554). The 'hunching' component has, however, also been described for bipedal and sitting positions, and in the wild, chimpanzees assume the posture in multiple contexts, ranging from aggression to greeting and courtship (Goodall 1986; Nishida *et al.* 1999), where it signals intense attention. While the co-occurrence of 'hunching' and attention following does not alone allow for differentiation, as to whether this behavioural

component is a purely adventitious cue of intense attention deployed by conspecifics, or if it involves voluntary and intentional components, the consistent assuming of the posture in the presence of conspecifics (and when in the presence of non-attentive conspecific, prefacing it by an auditory behaviour), suggests that the behaviour may have been produced intentionally and carried a communicative function. Overall, the results suggest that, when preceded by an auditory cue and accompanied by gaze alternation between the stimulus and a conspecific, the posture carried a communicative function to direct conspecifics to the novel, distal stimulus.

As predicted, there was no difference between the production of visual non-stimulus directional behaviours (arrest current behaviour, bipedal swagger, shake arm or leg silently, bob head, move head back rapidly) when the chimpanzees viewed the stimulus alone or in the presence of an attentive or non-attentive conspecific, nor did non-stimulus directional behaviours increase the probability of conspecifics co-orienting to the communicators' attention. Contrary to prediction, however, there was also no difference in the probability of chimpanzees approaching the stimulus when viewed in the presence or absence of a conspecific.

The chapter *indirectly* examined the suggestion that apes may use gaze as a communicative signal (de Waal 2001) by examining the communicators' gaze behaviour after looking to the stimulus, and the targets' response thereto. There was, however, no evidence that the chimpanzees used gaze as a communicative signal. Chimpanzees were no more likely than chance to look referentially to the conspecific (gaze behaviour: stimulus-conspecific-stimulus), nor to produce an auditory cue and subsequently shift gaze from the stimulus to the target and back to the stimulus, while being within the conspecific's 'open' or 'peripheral' field of vision; Nor did these behaviours influence the probability that conspecifics looked to the stimulus area.

Chimpanzee communicators were more than twice as likely to produce an auditory behaviour in experimental trials where a conspecific faced away rather than towards them, and more than six times as likely to do so than when they viewed the stimulus on their own. While these differences failed to reach statistical significance[31], significance was approached for the condition, in which communicators viewed the stimulus in the presence of a non-attentive conspecific ($p = 0.079$). While it is difficult to unequivocally determine if some of the chimpanzees intentionally produced auditory cues, so as to call conspecific attention, the overall trend of selectively producing auditory cues the presence of a non-attentive conspecific,

[31] Some individuals consistently, selectively produced auditory behaviours when viewing the stimulus in the presence of a non-attentive conspecific, while others never produced any auditory behaviours. The inferential statistics used controlled for individual contribution to the dataset, and thereby yielding results that only approached significance.

suggests that the auditory cues may have been produced intentionally and carried a communicative function, rather than being side effects of a response to the stimulus, driven mainly by arousal and emotional states.

It is, nonetheless, possible that in situations of uncertainty, arousal levels are reduced when conspecifics are present, and indeed facing towards rather than away from the individual (i.e., the presence and attention of a conspecific may provide some form of comfort). If so, it is possible that communicators may have experienced comparatively higher stimulus-induced arousal levels in the experimental condition, where a conspecific faced away from rather than towards the subject. Hence, while the higher proportion of auditory cues followed by stimulus directional cues in the 'facing away' condition may reflect an intention to inform conspecifics about the stimulus (high level interpretation), or, (as seems more plausible in the light of the paucity of reported cases of informative and declarative pointing in intraspecific ape communication), to direct the conspecific to the stimulus for social referential purposes, it is conceivable that the cue combination may be attributable to increased arousal levels in this condition. The trend towards producing directional visual cues when viewing the stimulus in the presence of an initially away-facing rather than towards-facing individual indirectly supports this. Alternatively, it may simply be that individuals increased their communicative efforts when faced with a non-attentive conspecific.

The trend towards selective production of auditory cues when in the context of a non-attentive conspecific is consistent with the finding that (a much larger group of) chimpanzees used auditory cues to capture the attention of non-attentive humans in imperative food-begging contexts, and produce attention 'getting sounds' ('raspberries' and extended grunts) when a human was present in combination with food, and not when either the food or human was presented alone (Hopkins *et al.* 2007).

There was no species-wide evidence of auditory signalling followed by directional visual signalling when the chimpanzees viewed the stimulus in the presence of a non-attentive conspecific. There were, however, noticeable individual differences, as some chimpanzees consistently led conspecifics to the stimulus, while others ignored it. During experimental trials where the target faced away from the communicator, two individuals consistently ($n = 5$) preceded a directional behaviour by an auditory behaviour. Moreover, in these trials one of the subjects (the dominant male of one population) produced an auditory behaviour and subsequently hand-gestured and/or leaned in the direction of the stimulus, while alternating gaze between the stimulus and conspecific, and stopping only when the conspecific leaned over

to look to the stimulus area (located on a branch facing away from the conspecific). Overall, the results suggest that *some* chimpanzees may combine functionally different cues from different modalities to direct conspecifics to a yet unseen novel stimulus. Thus, the compound category 'stimulus directional behaviour' may represent a case of a naturally occurring (albeit rarely deployed) intentional, declarative-like behaviour.

Previous research has suggested that apes do not solicit the attention of non-attending human experimenters (in a food begging experiment) and conspecifics (based on a 75 hour observational study of chimpanzees) before producing a more specific visual behaviour, but tend to first locomote into the visual field of the recipient (Liebal *et al.* 2004a,b). In contrast, there are reports of three language-trained chimpanzees calling the attention of humans before using visual gestures (Krause & Fouts 1997; Menzel 1999), and of a repeated calling and pointing sequence observed in one wild bonobo (Veà & Sabater-Pi 1999). The language-trained apes and those in the present experiment differ from the subjects in Liebal and colleagues' study in terms of rearing histories of close emotional bonding with the recipients. This suggests that some of the negative findings from laboratory experiments, where apes communicate with humans, may lie not in cognitive capacity, but in motivation (see Gómez 2004, for a similar argument regarding the performance of human-reared vs. group-reared chimpanzees during interactions with humans). The implication is that care should be exercised when attributing socio-cognitive performance to species differences, without careful consideration of ontogeny and motivational factors.

The typically negative results for apes' understanding of cooperative human referential gazing and pointing in the object-choice task have lent support to the notion of a cognitive difference between humans and other apes in terms of the ability to share intentions (e.g., Tomasello & Carpenter 2007). The present results, however, suggest that some chimpanzees may be able and motivated to solicit and direct conspecifics to novel, distal objects in non-competitive communicative contexts. While the experiment was designed to limit imperative motives, it did not eliminate the possibility of a selfish interrogative social referencing motive. Social referential pointing is neither about spurring the other into action to obtain a specific object or behaviour for the individual itself (imperative), nor to express or share interest or provide information ('high-level' cognitive interpretation of declarative pointing), but to provoke a response that can be used to discern ambiguity in situations of uncertainty and provide information about an object/situation and how to respond. When exposed to a novel object human-reared chimpanzees look referentially at their caregivers and adjust their behaviour according to the valence of the message they receive (Russell *et al.* 1997). Social referential *pointing*, however, includes first directing others to the referent, which, minimally, implies that individuals conceive

others as having emotional and/or behavioural responses towards the environment, that can be elicited by manipulating their attention. The present design did not address the question of whether the apes behaved to influence others' mental states (an aspect frequently included in more recent definitions of the term 'declarative' [to *share* attention, attitudes, emotions and experiences with the addressee: Tomasello 1999; Liszkowski *et al.* 2004]), or to evoke an attentional and/or emotional reaction as reflected in overt manifestations. In the light of past research, however, it seems reasonable to conclude that apes, under some circumstances, may direct conspecifics to hidden or novel objects for 'selfish' reasons (i.e., not necessarily for cooperative purposes), to elicit an attentional response (as reflected in overt manifestations [facial expressions, postures etc.]) that may be used to disambiguate the situation (see also Gómez *et al.* 1993). That is to say, minimally, the present results suggest that some of the chimpanzees engaged in intraspecific 'social referential pointing'.

Along with experiments showing that apes perform better in object-choice tasks when a gaze direction cue is combined with e.g., a vocalisation (Itakura *et al.* 1999; Call *et al.* 2000), the present finding that the chimpanzees may have used subtle, compound, and in some cases multi-modal, behaviours to follow and direct others to distal locations, suggests that 'pointing' in apes involves elements other than the arm and index finger, and lends support to the notion that apes may point with their entire bodies (Menzel 1973). This accords with naturalistic observations of human infant pointing, which is typically combined with other gestures, gaze alternation and vocalisations (Zinober & Martlew 1985). Intra-specific functional manipulation of others' attention may thus have been overlooked because it may be expressed through multiple, inconspicuous and composite behaviours that involve auditory gestures, the head and the whole body rather than a specialised species-specific referential signal.

CHAPTER 4: An exploratory observational study of chimpanzee attention management and manipulation

Summary

This exploratory study tested the hypothesis that chimpanzees accord and receive attention following as a function of rank. Approximately 15 hours of video-taped chimpanzee interactions were assessed for attention following instances, which were corrected for observation time per individual (seven adults and three infant chimpanzees), by dividing the number of times (i) the animals' attention was followed, and (ii) the animals followed another's attention, respectively, by the number of minutes of observation. Chimpanzees were more likely to follow the attention of the dominant individual, who in turn, was less likely to follow the attention of other chimpanzees (z-score for distance to the centroid = 1.98). These results provide the first evidence in support for the operation of the 'Social Attention Hypothesis' in chimpanzees, and suggest that the predictions made by the hypothesis (that individuals accord and receive attention as a function of rank: Chance 1967) also apply to the attention following. Moreover, eighty-four hours video taped chimpanzee interactions were analysed for the occurrence of 'hunching' behaviours (identified as potential 'pointing behaviours' in the previous chapter), which occurred four times and only in the context of attention following.

4.1 Introduction

Attention following & the direction of attention

While visual information can be communicative (designed to influence the behaviour of others), most is purely adventitious, and influences the observer's behaviour unintentionally, without codified signals (Gómez 1994; Watts 1998). The visual attention of conspecifics may afford subtle signals, and indicate interest in the environment (humans: Argyle & Cook 1976; non-human primates: Miller 1971, cited by Kaplan & Rogers 2002), and the focus of attention within a group therefore (i) reveals the cues that individuals attend to and which may be used to

predict their behaviour, and (ii) supplies attention following individuals with a cue for determining the main feature upon which inter-relationships are based (e.g., rank and relatedness).

Animals are predicted to reduce outward anti-predator vigilance in the safety of large groups, due to shared vigilance (Bednekoff & Lima 1998), dilution of risk (Hamilton 1971) and cooperative defence (e.g., Pulliam 1973). In contrast to most species of birds and mammals, who show a 'group size effect on vigilance', and decrease scanning rates with increasing group size (Elgar 1989; Quenette 1990), the majority of primates do, however, not support this notion (black howler monkeys, *Alouatta pigra*: Treves *et al.* 2001; red colobines, *Procolobus badius*, and redtail monkeys, *Cercopithecus ascanius*: Treves 1998; white-face capuchins, *Cebus capucinus*: Rose & Fedigan 1995; yellow baboons, *Papio ursinus*: Cowlishaw 1998)[32], but spend a considerable amount of time monitoring associates within their own groups (baboons: Cowlishaw 1998; gorillas: Watts 1998; red colobus and redtail monkey: Treves 1999; squirrel monkeys, *Saimiri sciureus*, & tamarins, *Saguinus labiatus*: Caine & Marra 1988). Indeed, three, five and seven observations of three chimpanzees (Treves 1997) suggest that chimpanzees increase vigilance (defined as "any visual search directed beyond arm's reach": Treves 1999, p. 117) with increasing group size. Moreover, although a larger, controlled study found no relationship between vigilance and group size, male (though not female) chimpanzee vigilance increased as the number of individuals within 3m increased (Kutusake 2006). Such absence of a reduction in vigilance with increasing group size may owe to that (a) a reduction in outward anti-predator vigilance is compensated by an increase in an alternative component of vigilance, such as monitoring associates, and/or, relatedly, (b) that the selective pressure imposed by predation is eclipsed by intra-group competition in chimpanzees. Thus, in primates total vigilance may not reflect group size, but variables indicating or affecting social interaction, such as the presence and proximity of conspecifics in general, and of higher-ranking individuals in particular. Moreover, for captive animals anti-predator vigilance in likely to be reduced, thereby increasing the proportion of time available for monitoring conspecifics.

Many organisms process eye information without reference to mental states, and rapidly follow the direction of others' gaze in a way suggesting a social reflex. Such reflexive gaze following, however, involves voluntary components related to e.g., relative status; Although, for example, low-status rhesus macaques reflexively follow the gaze of all familiar conspecifics, high-status macaques tend follow the gaze of only other high-status individuals (Shepherd *et al.* 2006). This accords with the 'Social Attention Hypothesis', which proposes that individuals

[32] Group sizes examined range between 2-76+ individuals.

accord and receive attention as a function of rank (Chance 1967; Chance & Jolly 1970). While, however, this hypothesis has received wide theoretical support, and the attention structures of captive gorillas (Yamagiwa 1992), wild patas monkeys, *Erythrocebus patas* (McNelis & Boatright-Horowitz 1998) and baboons, *Papio hamadryas* (Kummer & Kurt 1963) are based on social dominance, empirical evidence for its operation in chimpanzees, is nonexistent.[33]

Stimulus directed cues

Experimental manipulations (see Chapters 2 and 3) suggest that chimpanzees may use a 'hunching' posture (an action-based behaviour, in which the animal rounds its back, draws its head into its shoulders, leans its body forward and pushes its chin forward) to direct conspecifics to distal stimuli. In 12 trials (11 experimental trials where chimpanzees viewed a stimulus in the presence of a conspecific, and one control trial where a chimpanzee viewed the stimulus alone) six individuals adopted a 'hunching' posture, and in 75% of cases, preceded it by an auditory behaviour. Moreover, conspecifics were more likely to look to the stimulus when communicators adopted a 'hunching' posture. The 'hunching' behaviour is similar to the 'quadrupedal hunch', described as a "high-intensity threat display to an opponent who is equal or near equal, and an attack may come after this" (Estes 1991, p. 554). As the laser stimuli used the experiment detailed in Chapters 2 and 3 may have evoked alarm in the subjects, the frequency and contexts, in which 'hunching' and other stimulus directional behaviours occur during natural chimpanzee interactions, should be ascertained.

Aim

The aim of the study was three-fold; (i) to apply Chance's (1967) 'Social Attention Hypothesis' that individuals accord and receive attention as a function of dominance rank to attention following, and test the hypothesis that the chimpanzees followed the attention more frequently of the dominant individual (the alpha male) than of other individuals, (ii) to examine the cues that individuals produce prior to and during attention following, and (iii) to examine the prevalence of 'hunching' behaviours during natural chimpanzee interactions, and whether such co-occur with particular stimuli or events, and provoke noticeable changes in conspecifics' behaviour. The present study was based on data extracted from 84 hours video-taped chimpanzee interactions, wherefrom attention following episodes were recorded *ad libitum*. i.e., analyses were conducted post-hoc. The study is therefore exploratory.

[33] Unreferenced claims (by researchers studying orangutans: Kaplan and Rogers 2002) have, however, been made that lower ranking chimpanzees look more towards higher ranking individuals than *vice versa*.

4.2 Methods

4.2.1 Participants

Video was coded for seven adult and three infant chimpanzees housed at Copenhagen Zoo (see Chapter 2 for subject and housing details). For statistical purposes adult animals were considered individually, while the data for the infants were collapsed due to the comparatively shorter observation time of the infants.

4.2.2 Procedure and Statistics

Eighty-four hours of video recorded chimpanzee interactions were examined for the occurrence of 'hunching' behaviours, and of these approx. 15 hours (14.58 hours) were assessed for attention following episodes. Sequences analysed for attention following ranged from 30s to 8 minutes and were selected for analysis if the faces and relative foci of attention of two individuals could be unambiguously scored for a minimum of 30s. The duration of time analysed differed across individuals, ranging from 47 to 175 minutes for a low and high-ranking female, respectively. Instances of attention following were corrected for observation time per individual or class of individuals (infants), by dividing the number of times (i) the animal(s)' attention was followed, and (ii) the animal(s) followed another's attention, respectively, by the number of minutes of observation. Z-scores were computed to assess differences across animals in terms of being the producer and recipient of attention following. To test the hypothesis that the attention of the highest ranking individual (the alpha male) was followed more frequently than the attention of others', and that the individual was less likely to follow the attention of others, each animal's distance to the geometrical centroid (the geometrical centre of a scattergram, in which production and according of attention following was plotted on the x-axis and y-axis, respectively, see Figure 4.2 for clarification) was calculated, using the following formula: $\sqrt{(x - \bar{x})^2 - (y - \bar{y})^2}$. To determine significance, the z-score for each individual's/group's distance to the centroid was computed, to explore if the attention followed/following of each individual/group (as measured by their z-score) was significantly further away from the centroid than would be predicted by chance.

4.2.3 Inter-rater reliability

I coded the videotapes and recorded 46 cases of attention following. A second rater assessed all 46 cases for inter-observer reliability and agreed that in 98% (45 of 46), the video clips contained an instance of attention following[34]. The case, on which coders disagreed, was excluded from analysis.

4.2.4 Behavioural coding

Where relevant, the definitions were as in the experimental procedure detailed in Chapters 2 and 3. For example, the animal, whose focus of attention was followed, was termed the 'communicator', the animal that followed another's focus of attention was termed the 'target', and the object/event that the communicator looked to, was termed the 'stimulus'. Only cases of attention *following* were included, i.e., co-focus arising from a series of independent stimulus-driven events (such as noise) were excluded. A behaviour was scored as attention following if chimpanzee 'A' looked in the direction of chimpanzee 'B's attention within 2s of looking to chimpanzee 'B', with both head and eyes simultaneously. For clarity, only attention following to locations distal to the communicator was recorded; I.e., looks to the communicator's face, immediately followed by a look anywhere else on the communicator's body (even if this is where communicator and target clearly looked), were excluded.

The communicator's and target's behaviour was coded from 10s before the start of observed attention following instances, and are detailed in table 3.1 (Cue definitions and Classes, Chapter 2). The behaviours consisted of (1) auditory behaviours (vocalise, clap, stamp or knock on the ground, audibly move object), (2) visual non-stimulus directional behaviours (arrest current behaviour, bipedal swagger, shake arm or leg silently, bob head, move head back rapidly), (3) visual stimulus directional behaviours (touch, lean torso towards, move extremity or head in the direction of the stimulus, (4) locomotory stimulus directional behaviour (approach stimulus area), (5) conspecific directed behaviour (instances where the communicator shifted gaze from the stimulus to the conspecific and back to the stimulus [gaze sequence: stimulus – target – stimulus]), and (6) 'hunching'. In addition (7) cases of target gaze alternation (gaze sequence: communicator – stimulus – communicator) were recorded. Only trials in which the animal's attentional behaviour could be reliably coded were included. Cues were analysed as part of a cue category, apart from conspecific directed cues, which were analysed individually. In addition, the number of individuals in the enclosure, the distance between the communicator

[34] The percentage of agreement is presented rather than the conventional Cohen's Kappa value, which requires a dichotomous variable (i.e., it would require that the raters recorded instances of absence as well as presence of attention following).

and target (< 1m, < 2m, < 3m, < 4m), and the general behaviour were recorded (Forage: search, handle, consume; Groom: being groomed, grooming conspecific, self-grooming, Play: playful interaction with conspecific; Aggression: aggressive interaction with conspecific; Idle: animal does not exhibit active behaviour, including sitting, laying and staring into space).

4.3 Results

4.3.1 The direction of attention following

Forty-five instances of attention following were recorded during 14.58 hours of analysed chimpanzee interactions. The communicators' behaviour during the time of attention following was classified as idle (64.44%), forage (15.56%), groom (13.33%), locomote (4.44%) and play (2.22%), and inter-animal distance ranged form 1 to 4 meters, with 2-4 animals in the enclosures (in most cases the observations with more than 2 animals in the enclosure owed to the presence of infants that nearly always accompanied their mothers).

Instances of attention following were corrected for observation-time per individual or class of individuals (Table 4.1 and Figure 4.1). The geometrical centroid (i.e., the geometrical centre of a scattergram, in which the production and according of attention following was plotted on the x-axis and y-axis, respectively) was 0.05 x 0.05, signifying the geometrical point at which individuals were equally likely to accord and receive attention following. The z-score for each animal's distance to the centroid was computed. The alpha male (Carl) was significantly more likely to have his attention followed and less likely to follow the attention of a conspecific than other group members were (Carl, $z = 1.99$, $p = 0.05$, Figure 4.2).

Table 4.1: Observation time and attention following accorded and received per individual. For each individual instances of attention following were corrected for observation time, and the z-score for the distance to the centroid is shown.

	Minutes observed	Instances of attention followed	Instances of following anothers' attention	Frequency of attention being followed per minute	Frequency of following another' attention per minute	Z-score for individual distance to the centroid
Carl (alpha male)	115	13	2	0.11	0.02	1.99
Cindy	175	5	12	0.03	0.07	-0.04
Gigi	91	4	4	0.04	0.04	-0.90
Infants (3)	141	8	6	0.06	0.04	-0.72
Mati	47	0	2	0.00	0.04	0.95
Olga	114	7	6	0.06	0.05	-0.65
Trunte	97	3	7	0.03	0.07	0.01
Yoran	95	5	6	0.05	0.06	-0.64

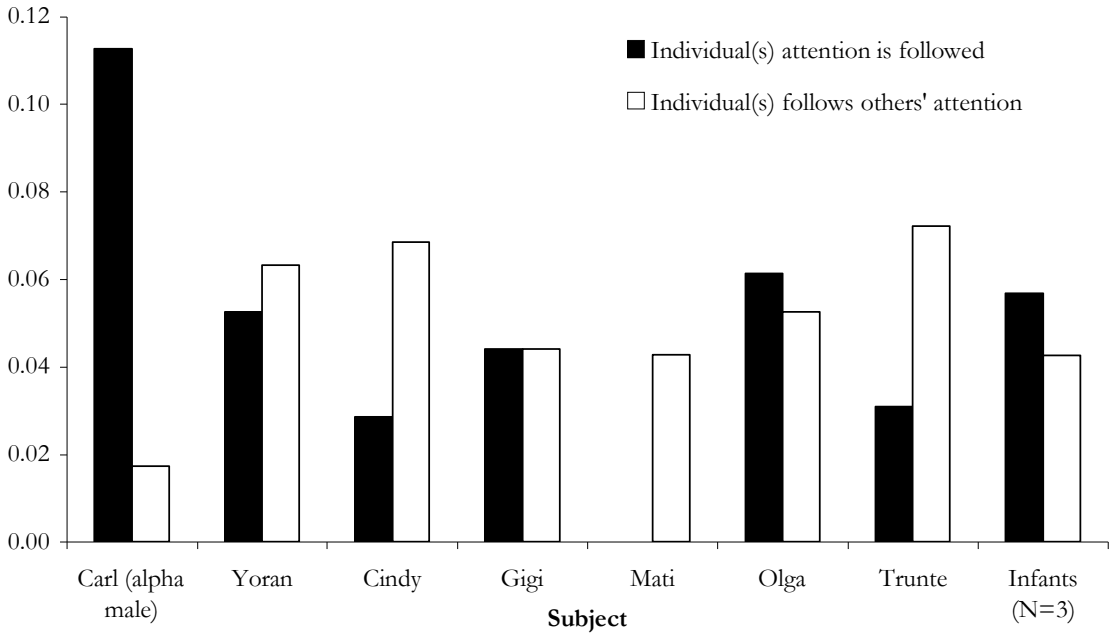


Figure 4.1: Attention followed and following. Proportion of attention followed and attention following, corrected for observation time.

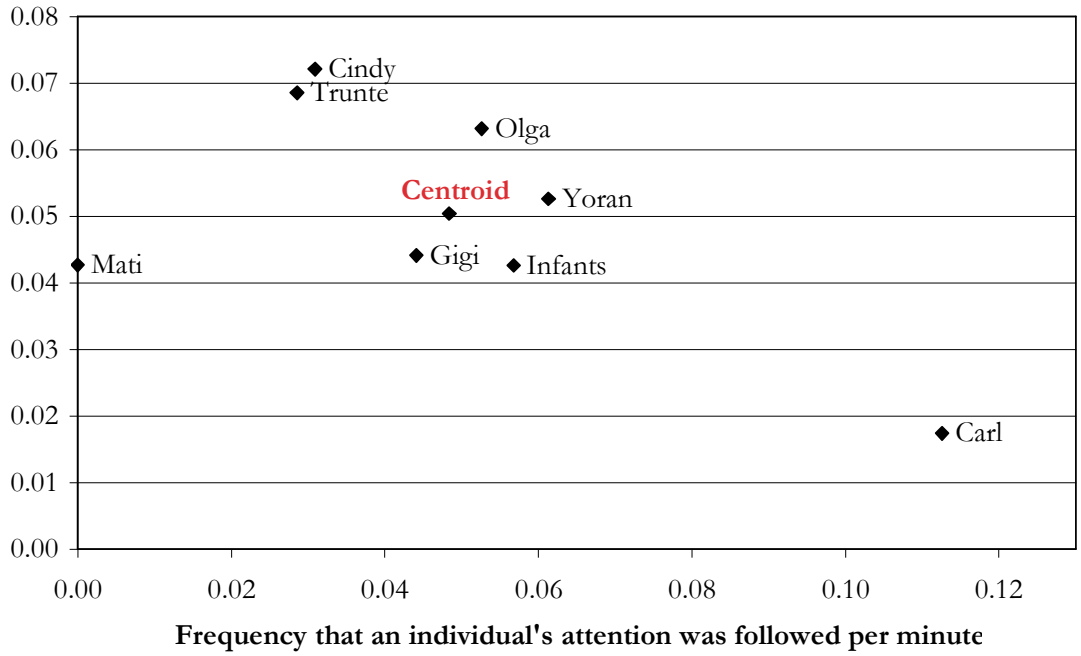


Figure 4.2: Attention followed and following per individual/class of individuals, corrected for observation time.

4.3.2 Cues associated with attention following

No auditory or tactile behaviours were observed during 45 instances of attention following. The cues most frequently performed by communicators were visual non-stimulus-directional cues (arrest behaviour [N = 9], move head back rapidly [N = 4], bob head [N = 3]), followed by stimulus directional cues (lean towards [N = 8], and move head forwards in direction of stimulus [N = 7], Figure 4.3). Targets shifted gaze between the communicator and stimulus in 25% (11 of 45) of attention following episodes, and in 13% (6 of 45) the communicator shifted gaze between the stimulus and target (for an example, see Figure 4.4).

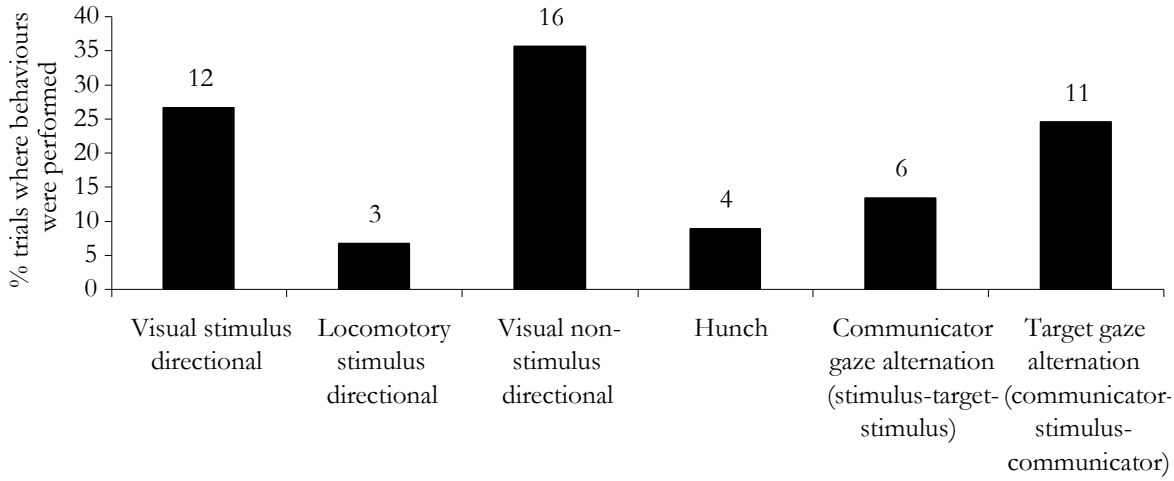


Figure 4.3: Behaviours associated with attention following. Percent attention following episodes (N = 45) where communicators and targets (last column only) performed various behaviours.

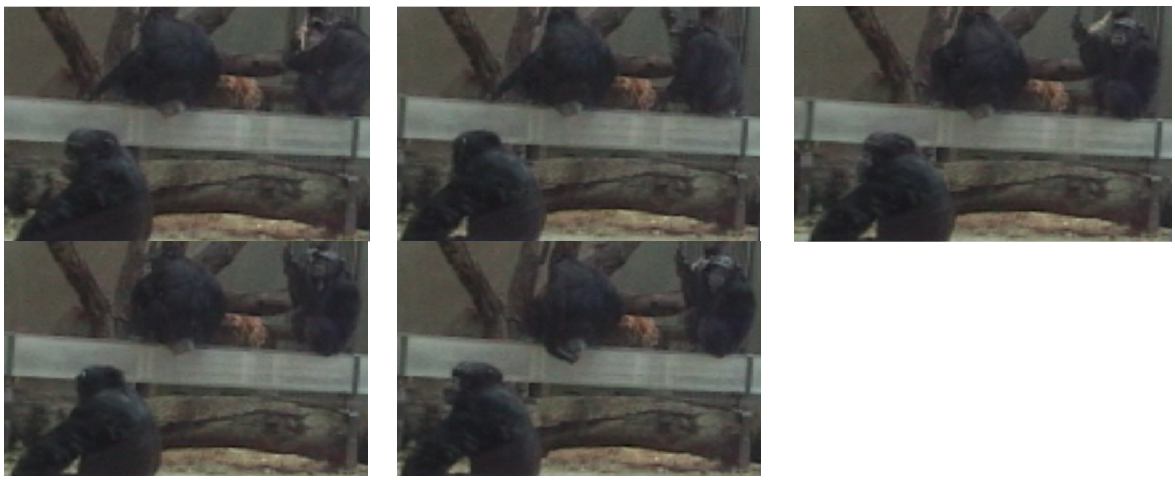


Figure 4.4: Stills of attention following episode involving repeated gaze alternation. From top left: alpha male (bottom left in stills) entered the enclosure and (within the following 10s) looked out of the window; then looked to conspecifics; looked out of the window; looked back to conspecifics (2nd time) and out of the window (3rd time). Conspecific (top right in stills) looked to the alpha male, leaned towards the window, and looked in the direction of the alpha's attention.

4.3.3 The occurrence of hunching behaviours

Four instances of 'hunching' were observed during 84 hours of observation. In all cases a conspecific looked to the 'hunching' animal and subsequently towards the object of the 'hunching' animal's attention. The dominant male adopted a 'hunching' posture three times and an infant once (Figures 4.5 – 4.8). No sounds were audible from the direction that communicators looked and no conspecifics were visible. In no case was identification of the object of the communicator's focus possible.

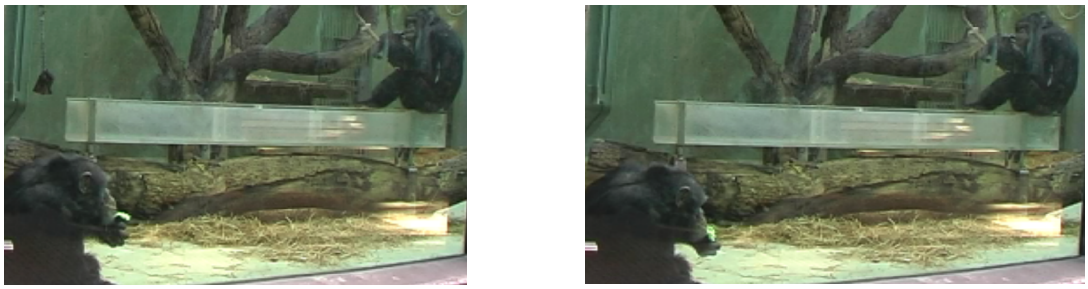


Figure 4.5: Sitting 'hunch'. The alpha male (bottom left) sits looking through the door to another enclosure, which has a window to the outside public areas (approx. 30m from the alpha male). The beta male (top right) turns its head and looks to the alpha, who then looks to beta, then lowers its head into its shoulders to sinks slightly forward into a 'hunching' posture and looks back through the door. The beta male turns around (repositions its body), looks through the door for 14s and then back to the alpha male.

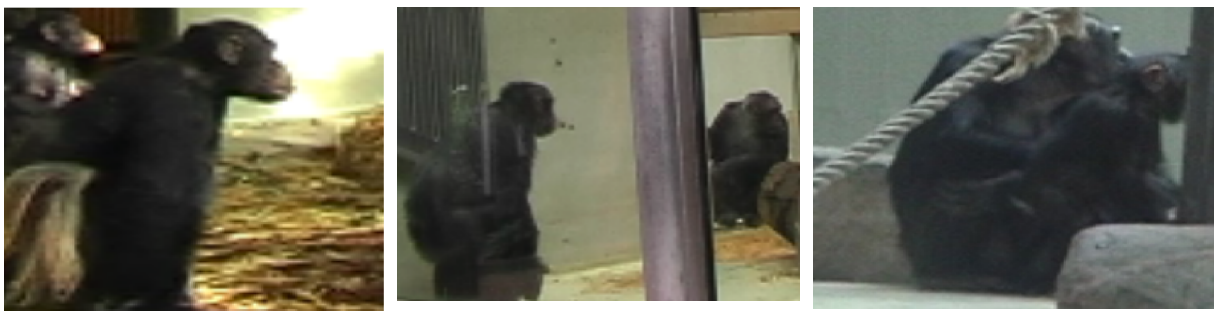


Figure 4.6-4.8: Quadrupedal and bipedal 'hunching' behaviour. From left: (i) alpha male enters enclosure, looks around and towards the ceiling, adopts a quadrupedal hunching posture and looks towards a window approx. 20m away. Conspecifics look to the alpha male and then towards the window (no sound were audible from the direction of the window, nor were any people visible). (ii) The alpha male (left) looks to a female conspecific (right) who faces him, moves into a bipedal 'hunching' posture, looks towards a door to an adjoining enclosure. Target turns around and looks in the same direction. (iii) Infant sits, then stands up, moves into a bipedal hunch while looking towards a wall, the infant then to looks to its mother, and then towards the wall. The mother co-orients to the wall.

4.4 Discussion

The study aimed to apply Chance's (1967) hypothesis that individuals accord and receive attention as a function of dominance rank, to attention following. Chimpanzees were more likely to follow the attention of the alpha male, who in turn was less likely to follow the attention of others. The 'Social Attention Hypothesis' is widely supported by evidence for its operation in a number of primate species, however, empirical data have thus far lacked for chimpanzees. While the hypothesis is traditionally tested by measuring the number of glances and duration of looks to conspecifics, attention following is a plausible extension of the predictions made by the hypothesis. Indeed, the present results are consistent with the finding that reflexive gaze following of macaques is gated by social dominance (Shepherd *et al.* 2006). While the opportunistic nature of the data collection (*ad libitum* data collection from videos, and consequent unequal observation time across individuals) means that the study remains exploratory and the results conditional upon further confirmation, they provide the first evidence for the operation of the 'Social Attention Hypothesis' in chimpanzees and suggest that the predictions made by the hypothesis also apply to the attention following.

The present results are consistent with the suggestion that low social status may be associated with increased arousal and scanning behaviour (e.g., Caine & Marra 1988), and consequently increased levels of attention following. Several researchers (e.g., Keverne *et al.* 1978; Shepherd *et al.* 2006) have, however, suggested that high social status requires selective monitoring of only other high status individuals; a suggestion to which the present results do not lend support, as the only two cases of recorded attention following by the alpha male were to two low-ranking females.

The study also examined the cues that chimpanzee communicators produce prior to and during attention following episodes, and the contextual occurrence of 'hunching' behaviours. None of 45 attention following episodes involved auditory behaviours, yet many were preceded by non-stimulus- and stimulus directional behaviours (e.g., leaning and moving the head forwards towards the stimulus). The approx. 84 hours of analysed chimpanzee interactions, contained four instances of the 'hunching' posture, which all led conspecifics to co-orient to the communicators' direction of attention. The co-occurrence of 'hunching' and attention following does not alone allow for differentiation, as to whether the behavioural component is a purely adventitious signal of intense attention (as suggested by Estes 1991) that is deployed by conspecifics as a sign of something of potential interest, or if it involves voluntary and

intentional components on behalf of the communicator. Nonetheless, in conjunction with the trend for chimpanzees to adopt a 'hunching' posture when viewing a novel stimulus in the presence of a conspecific, and not when alone (see Chapter 3 Chimpanzee Attention Manipulation[35]), and that conspecifics were more likely to co-orient to the communicator's attention when the 'hunching' posture was adopted, the present finding goes some way to suggest that this (albeit very rare) behaviour may be involved in attention coordination contexts.

Several things suggest that the chimpanzees were aware that others' attention was directed at specific events in the environment. For example, targets alternated gaze between the communicator and the direction of the communicators' attention in 25% of attention following episodes, and in 13% (6 of 45) the communicator repeatedly (up to 3 times) shifted gaze between a conspecific and the object of its own attention. There was thus some suggestion that communicators either 'checked' conspecifics' attention, attempted social referencing, or may (in a small number of cases) have used head/gaze shifts between the conspecific and 'stimulus', as a communicative cue. While such repeated head/gaze shifts', is consistent with the suggestion by de Waal (2001) that apes may use gaze to communicate referentially about external events, any conclusions are constrained by the nature of the data collection (examination of attention following episodes), which naturally meant that all triadic gaze exchanges between communicators, targets and external stimuli led to visual coorientation. The experimental manipulation reported in Chapter 3 also showed that communicators frequently (in 61% of trials that could be reliably scored for gaze changes, n = 23), shifted gaze between the stimulus and target conspecific and back to the stimulus, and in 75% (n = 8) of trials where communicators produced an auditory cue, shifted gaze between the stimulus-target-stimulus within a few seconds, while being within the conspecific's 'open' or 'peripheral' field of vision. The lack of evidence that such repeated head/gaze shifts (in the experimental manipulation) increased the probability that target conspecifics co-oriented to the laser stimulus, however, suggests that even if the chimpanzees used gaze shifts as intentionally communicative behaviours to direct others' attention to distal locations, they not be particularly effective cues.

While research has often relied on gaze alternation as a criterion for intentional communication, and pointing has been classified as non-communicative when not accompanied

[35] While chimpanzees were *not* significantly more likely to adopt the hunching posture when viewing the stimulus in the presence of a conspecific than alone, there was a clear trend, with the difference between the production of the behaviour in social and non-social conditions very closely approaching significance ($p = 0.056$).

by gaze alternation to a recipient (Bates *et al.* 1975), it may be misleading to use coordinated looks as the primary criterion for communicative intent (Liszkowski 2005). Not only is there evidence of cross-cultural differences in the degree of e.g., mutual gaze in human mother-infant dyads (with twice as much face-to-face engagement in North American, compared to Japanese, mother-infant dyads: Bornstein *et al.* 1990, cited by Blake *et al.* 2003), but studies have also reported low levels (17%) of eye contact/checking co-occurring with communicative gestures in 9-14 months old Japanese infants (Blake *et al.* 2003). Absence of gaze alternation does not necessarily imply absence of communicative intent, as individuals (be they apes or human infants) may simply assume that the context presupposes an assumption of communicative intent, and that the viewer understands that the subject's behaviour is intended as communicative (e.g., Bard 1992; Liszkowski 2005). More research, including cross-cultural studies of adult and infant humans, is needed to clarify whether the use gaze alternation as a central criterion to indicate communicative intent is warranted.

CHAPTER 5: Attention following in bonobos

Summary

While the genetic proximity of the *Pan* species may suggest similar attention following and directing skills, differences in social behaviours, such as cooperation, raise the question, as to whether the species may exhibit different motivations to follow others' attention. The present study tested the hypothesis that experimentally naïve bonobos follow the attention of conspecifics to locations behind themselves and around barriers, and lead non-attentive conspecifics to detect a novel object. Eleven bonobos were presented with a novel visual stimulus to test if they would lead a non-attending conspecific to detect it under two experimental conditions. In one the conspecific faced the communicator, while another required the communicator to first attract the attention of a non-attending conspecific. Some trials required targets to only turn to detect the stimulus, while others that they locomote around an obstacle to follow the communicator's attention (geometric attention following). Bonobos followed conspecific attention, and showed some indication of geometric attention following (as subjects passed tests conducted on only the first received trial, but failed tests including all trials that they received).

5.1 Introduction

Bonobos and chimpanzees diverged from the common evolutionary ancestor shared with humans 5 million year ago (Kumar *et al.* 2005) and are genetically equidistant to humans. Chimpanzees have long been considered *the* referential model for human cognition and behaviour, and have been studied extensively with respect to understanding of (primarily human) attention and referential gestures. By comparison bonobos are understudied, despite, by homology, equal value as a referential model. The *Pan* species diverged from each other as little as 0.9-2.7 m.y.a. (Bradley & Vigilant 2002; Kassmann & Pääbo 2002; Won & Hey 2005), however,

differ in aspects of social structure, temperaments, cooperation and possibly consequently, cognition (Stanford 1998; Boesch *et al.* 2002; Hare *et al.* 2007; Hare & Kwetuenda 2010).

Chimpanzees exhibit male dominance, with males forming long-term alliances to coordinate and dominate females and rivals. They cooperate during hunts, aggressive territory border patrols, infanticide and occasional lethal attacks on neighbouring group members (Goodall 1979; Boesch & Boesch 1989; Mitani & Watts 1999; Wrangham 1999; Boesch & Boesch-Achermann 2000; Watts & Mitani 2001; Watts *et al.* 2002). By comparison, male sociality is almost non-existent among bonobos, who exhibit female social dominance, with unrelated females forming strong social bonds against males, which via intra-sexual contact is thought to minimise aggression and dilute conflicts (Susman 1984; Kano 1992). The rate of intra-specific physical conflict and lethal violence is considerably lower among bonobos, with infanticide being rare (Hohmann & Fruth 2008), inter-group encounters predominantly amicable, and border-patrolling and inter-community raiding purportedly non-existent (Doran 2002). Overall, bonobos appear more egalitarian, tolerant and cooperative in their social interactions (Hare *et al.* 2007; Vigilant 2007), something, which may be related to the presence of a microsatellite DNA section controlling responses to vasopressin (a hormone affecting attachment and bonding) in bonobos (and humans), while being absent in chimpanzees (Hammock & Young 2005).

Chimpanzees perform better in competitive than collaborative tests of social cognition. To account for this difference, Hare and Tomasello's (2005) 'Emotional Reactivity Hypothesis' has proposed that apes' social problem solving may be constrained by temperament and disposition for cooperation and sharing. According to this hypothesis, selection for social emotions, that counteract competitiveness, favoured the emergence of stronger cooperative tendencies in bonobos than chimpanzees, as exemplified by the more relaxed social relationships of bonobos, including fewer and less intense conflicts over food (Hare 2007). The hypothesis has received some support from findings suggesting that bonobos outperform chimpanzees in cooperative tests. While pairs of either bonobos or chimpanzees will cooperate to achieve a goal that provides food for both partners, only bonobos cooperate when the food is indivisible and will end up monopolised by one partner (Hare *et al.* 2007). Moreover, when given an opportunity, unrelated bonobos prefer to release a conspecific form an adjacent room and feed together rather than eating alone (Hare & Kwetuenda 2010). The question arises whether the species exhibit different motivations in following and manipulating conspecific attention, and whether bonobos are more likely to lead conspecifics to view a novel stimulus.

Previous research, involving four bonobos with much human experience, suggests that bonobos are sensitive to the attentional states of humans and follow human attention to locations above and behind themselves and geometrically, around opaque barriers and through windowed obstructions (Kaminski *et al.* 2004; Liebal *et al.* 2004a; Bräuer *et al.* 2005; Okamoto-Barth *et al.* 2007a). Johnson and Oswald (2001) reported that bonobos follow the gaze of conspecifics, although the authors referred to papers (Johnson 1997; Johnson *et al.* 1999) that make not reference to observed instances of attention following.[36] A recent study modelled on Tomasello and colleagues' study of intra-specific gaze following (Tomasello *et al.* 1998), however, suggested that three bonobos followed the attention of conspecifics induced to raise their heads to locations 2m above and immediately behind the subject (Pitman & Shumaker 2009). The study, nonetheless, found that bonobos followed human attention more readily than conspecific attention (Pitman & Shumaker 2009).

While previous studies have found little evidence that bonobo coordinate looks between conspecifics and objects (Bard & Vauclair 1984), ape 'communicators' in this experiment were more likely to alternate gaze between the stimulus-conspecific-stimulus within a 10s period when the human experimenter held up an object than simply a empty hand (Pitman & Shumaker 2009).[37] Overall, this body of research suggests some understanding of the referential nature of gaze direction.

Bonobos are claimed to show social referencing (Savage-Rumbaugh 1986, cited by Johnson 2004), have some understanding that what others see influence their behaviour and behave differently when a human faces towards or away from them. For example, they preferentially use visual gestures to beg food from a human experimenter facing them, and locomote to places where the experimenter can see their gestures, when the experimenter faces away from them (Kaminski *et al.* 2004; Liebal *et al.* 2004a). These experiments have, however, used the same four bonobos, of whom three were human-reared and all had considerable experience with humans and the experimental setups (see Appendix 3). Observations nonetheless, suggest that bonobos are more likely to use visual than tactile gestures during interactions with attending conspecifics (Pika 2007).

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[36] "Captive bonobos (…), when mature, show gaze aversion, gaze following, and can use the eyes as a cue at close range (personal observation – see also Johnson 1997; Johnson *et al.* 1999)" (Johnson & Oswald 2001, p. 176).

[37] Pitman & Shumaker (2009) claimed that all the ape species (bonobos, chimpanzees, orangutans and gorillas) engaged in coordinated (triadic) communication with conspecifics, however, peculiarly, only reported data pooled for the four species, thereby preventing any assessment as to whether the coordinated looks were performed by e.g., bonobos.

The aims, predictions and general methodology of the present study correspond to those detailed in the chimpanzee attention following study (Chapter 2). The aims were to assess the conspecific gaze-following skills of bonobos, and to test the hypotheses that experimentally naïve bonobos are able and inclined to follow the attention of conspecifics (rather than humans) in a non-food related and non-competitive context, including under conditions that require geometrical attention following.

5.2 Methods

5.2.1 Participants

Participants consisted of 11 bonobos, ranging from 6 months to 28 years of age at the beginning of the experiment. There were four adult female bonobos and three males ranging from 10-29 years of age (mean age at the start of the experiment = 19.36 yr., s.d. = 11.07), one adolescent, and three infants (6-45 months). Three individuals were hand-reared and eight were parent-reared (Table 5.1). None of the bonobos had participated in behavioural experiments before, thus all were experimentally naïve. One individual (Cheka) was observed to over-groom herself and her infant (Gemena), but no other stereotypic behaviours were observed.

Table 5.1: Bonobo participants. The age classes follow those established by Thompson-Handler and colleagues (Thompson-Handler *et al.* 1984).

Individual	Sex	Age Class	Date of birth	Age at time of experiment	Rearing history	Mother
Banya	F	Adult	01-02-90	16-17 yr.	Parent	Bonnie
Cheka	F	Adult	18-03-96	10-11 yr.	Parent	Salanga
Diatou	F	Adult	21-10-77	28-29 yr.	Hand	Wilhelma
Jasongo	M	Adult	02-08-90	16-17 yr.	Hand	Lisala
Kakowet II	M	Adult	07-06-80	26-27 yr.	Hand	Linda
Keke	M	Adult	02-01-94	12-13 yr.	Parent	Diatou
Kichele	F	Adult	19-04-89	17-18 yr.	Parent	Diatou
Maringa	F	Adolescent	05-05-98	8-9 yr.	Parent	Yala
Luo	M	Infant	01-12-02	39-45 mts.	Parent	Diatou
Bokela	F	Infant	14-10-03	35-45 mts.	Parent	Banja
Gemena	F	Infant	07-11-05	6-21 mts.	Parent	Cheka

Husbandry

The bonobos were housed in two social groups at Twycross Zoo (England). During the day each group had permanent access (except during cleaning hours) to a core indoor enclosure (approx. 35 m^2) and between the hours of 7.30 and 16.30 the groups alternated access a semi-natural outdoor compound of approx. 600 m^2 (Figure 5.1). The outdoor enclosure contained a wooden climbing structure, two large tree trunks, rubber mesh and robes, and an artificial waterfall, yet provided few opportunities for natural foraging, as it contained no natural foliage, and the only growing plant was grass. All bonobos were observed to pick and eat grass. The keepers provided the apes with a variety of enrichment in the form of plastic bottles, cloth and boxes made from cardboard and plastic. The bonobos had auditory access to the public areas, as the outdoor enclosures were separated from these by a 4m deep moat and approx. 2m high glass windows. Neither indoor nor outdoor enclosures provided a place for the bonobos to be out of view of the public. The exhibit received the majority of its visitors between the hours of 11.30-14.00. Due to the exhibit's location (far from the zoo entrance), it received fewer visitors and was exposed to less noise than the exhibits of the orangutans or the chimpanzees tested at the same zoo. The animals were fed according to their daily routine on a variety of fruits and vegetables, supplemented by primate pellets, vitamins and diluted fruit drinks.

Figure 5.1: Experimental enclosure

5.2.2 Data collection

The bonobos were tested between the hours of 10.00-16.30 between April and October 2006, and between 07.30-16.30 between April and August 2007 during a total of approx. 900 observation hours[38]. Trials were mainly conducted outside opening hours and at times when fewest members of the public were present, between the hours of 7.30-11.30 and 14.30-16.30. The bonobos were tested exclusively in their outdoor enclosure and the experiment recorded by two camcorders (Panasonic NV-GS120 and Sony DCR-HC40/DCR-PC55E). The miniDV videotapes were digitised into IMovie and converted into QuickTime files, from which the trials were scored.

5.2.3 Design, materials and procedure

The general methods were as detailed in chapter 2, and consisted of the same two experimental conditions *('Target faces communicator'* and *'Target faces away from communicator')* and five control conditions *('No Stimulus-Towards', 'No Stimulus-Away', 'Target Alone', 'Target and Ignorant Communicator', 'Communicator Alone'*, Figures 5.2-2.8). The experimenter projected a visual stimulus into the participants' enclosure; a moving light pattern within an area of approx. 0.5m^2, produced by a commercial green laser pointer (OnPoint Extreme Fusion: 532nm, classification: 3b, power output: 125 mW, point diameter at 4m distance in ambient outside light: approx. 2cm). The stimulus was adapted to the brighter light conditions of the outside bonobo enclosures compared to the inside chimpanzee enclosures. The laser was more powerful than the laser used with chimpanzees participants onto which no optical diffractive element was attached (OnPoint GR532: 532 nm, classification: 2b, power output: 5 mW, point diameter at 4m distance: approx. 2cm), and identical to that onto which an optical diffractive element was attached, so it produced an image of an insect. The brighter outside light conditions meant that the stimulus size of the more powerful laser (OnPoint Extreme Fusion) was equivalent to the stimulus size of the less powerful laser (OnPoint GR532) used with chimpanzees.

[38] Bonobos and orangutans (Chapter 7) were tested during a total of 1,523 observation hours, of which approx. 60% of the time (914 hours) was spent with the bonobos and 40% (609 hours) with the orangutans.

Figure 5.2: Experimental condition: '*Target faces communicator*'. (Still of stimulus is encircled).

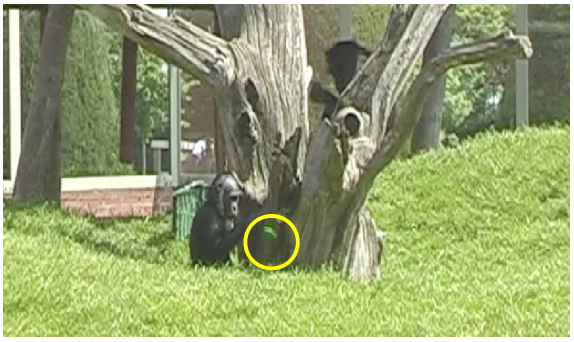


Figure 5.3: Experimental condition: '*Target faces away from communicator*'.

Figure 5.4: Control condition: '*No Stimulus -Target faces communicator*'. The stimulus is aimed on the tree in front of the communicator.

Figure 5.5: Control condition: '*No Stimulus – Target faces away from communicator*'. The stimulus is aimed on the ground behind the target.

Figure 5.6: Control condition: *'Target Alone'*.

Figure 5.7: Control condition: '*Target and Ignorant Communicator*'.

Figure 5.8: Control condition: *'Communicator Alone*'.

The stimulus was projected from the public areas onto 32 different locations in the experimental enclosure (Figure 5.9).

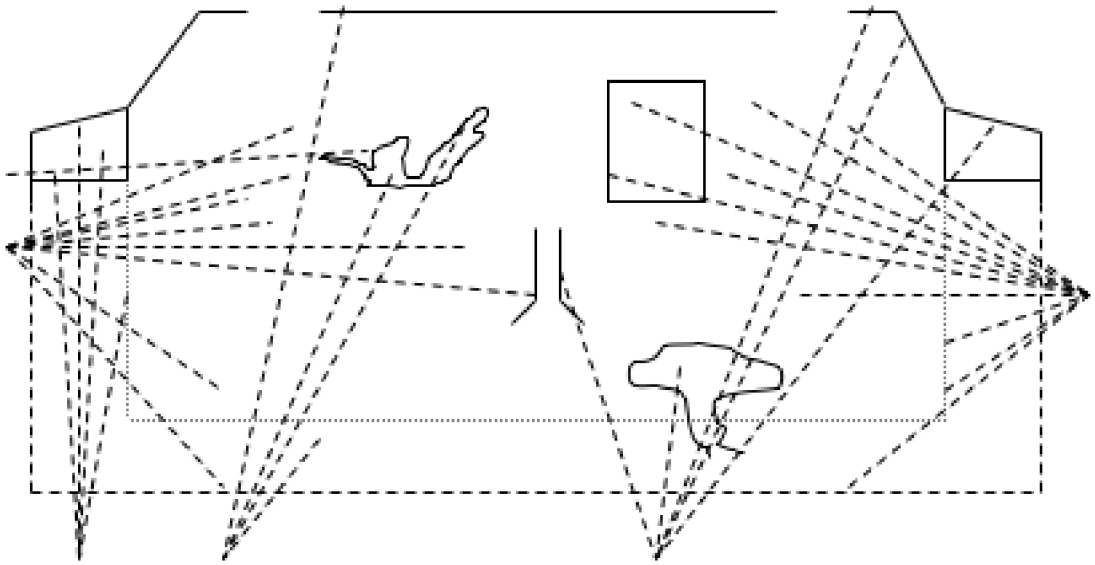


Figure 5.9: The use of the experimental enclosure. Dotted lines indicate windows and stimulus projection points at 32 locations, projected from the public areas. Broken lines show two doors to the inside enclosures (see also Figure 5.1). Illustrations (clockwise from left) depict a log, a climbing structure (see also Figure 5.1) a waterfall, and a tree.

Trials requiring targets to turn versus locomote to detect the stimulus

Twenty-two percent (31 of 139) of trials required targets to only *turn* around to look to the stimulus area, while 78% (108 of 139) that they first *locomote* around an obstacle (Table 5.2). The two trial types were not designed conditions, but due to the nature of the experimental set-up.

Table 5.2: Trials requiring targets to 'turn' and 'locomote' to look to the stimulus. The '*Experimental*' and '*No Stimulus*' conditions each consisted of two trial types.

Condition	**Percent**		**N**	
	Turn	**Locomote**	**Turn**	**Locomote**
Experimental	18	82	7	32
No Stimulus	45	55	18	22
Target Alone	19	81	4	17
Target and Ignorant Communicator	5	95	2	37
Total	22	78	31	108

Trial sequences

The conditions were presented sequentially in an order similar to that detailed in Chapter 2 (section 2.2.2.4 Trial sequences). Six participants received two trial sequences; one received two trial sequences bar one experimental trial, and two individuals received only one trial sequence (Table 5.3) Individuals who received one or incomplete trial sequences were young restive mothers (Banya and Cheka) and the offspring of one (Bokela).[39]

Table 5.3: Trial sequences and order of presentation of trials; EXP = '*Experimental*', NOS = '*No Stimulus*', TAR = '*Target Alone*', TAR+ = '*Target and Ignorant Communicator*', COM = '*Communicator Alone*', T = Target faces *towards* communicator, A = Target faces *away* from communicator. Coloured text indicates trials involving a stimulus, and trials highlighted were not conducted.

Individual	Trial Sequence	1	2	3	4	5	6	7	8
Banya	1	TAR+	TAR	COM	EXP T	TAR	EXP A	NOS T	NOS A
	2	TAR	TAR	NOS T	COM	TAR+	EXP A	NOS A	EXP T
Bokela	1	TAR+	EXP A	TAR+	NOS A	COM	EXP T	TAR	NOS T
Cheka	1	COM	NOS T	NOS A	EXP A	EXP T	TAR	TAR+	TAR
Diatou	1	COM	NOS A	TAR+	NOS T	EXP T	TAR	EXP A	TAR
	2	TAR	EXP T	EXP A	TAR+	TAR	NOS A	COM	NOS T
Gemena	1	TAR	TAR+	COM	EXP A	NOS T	EXP T	NOS A	TAR
	2	EXP A	EXP T	TAR	NOS A	TAR	NOS T	TAR+	COM
Jasongo	1	TAR+	COM	EXP T	NOS A	EXP A	NOS T	TAR+	TAR
	2	NOS A	TAR+	TAR	COM	EXP A	TAR+	EXP T	NOS T
Kakowet	1	EXP A	NOS T	TAR+	TAR	TAR	COM	EXP T	NOS A
	2	NOS T	EXP T	NOS A	TAR+	EXP A	TAR	COM	TAR
Keke	1	COM	NOS A	EXP T	TAR	NOS T	TAR	TAR+	EXP A
	2	TAR	NOS T	COM	EXP T	NOS A	EXP A	TAR	TAR+
Kichele	1	NOS A	TAR	EXP T	TAR	COM	TAR+	NOS T	EXP A
	2	TAR	EXP A	TAR	NOS T	TAR+	COM	EXP T	NOS A
Lou	1	TAR+	COM	EXP A	NOS T	EXP T	NOS A	TAR	TAR
	2	NOS T	TAR	NOS A	EXP A	TAR+	TAR	EXP T	COM
Maringa	1	COM	TAR	NOS T	TAR+	NOS A	EXP T	EXP A	TAR
	2	EXP T	NOS A	EXP A	TAR	TAR	NOS T	COM	TAR+

[39] Bokela received two trial sequences, yet the second sequence was excluded from the analysis due to experimenter error in experimental trials (both in which the target looked to the stimulus). In the *'facing towards'* trial it could not be conclusively determined that the target did not look to the stimulus before the communicator, and in the '*facing away*' trial, stimulus projection enabled the target to detect the stimulus origin and perhaps therefore locomote and look to the stimulus.

5.2.4 Scoring & reliability

All trials were scored from videotapes. I coded whether the stimulus area fell within targets' 'open' field of vision (for definitions, see Figures 2.12 and 2.14) during the pre-stimulus and stimulus phases, and a second coder coded 28% (39 of 139) of trials randomly selected from the dataset to assess inter-observer reliability. There was 97% agreement between the two coders in terms of target looks to the stimulus area in both the pre-stimulus (Cohen's kappa = 0.95 = good agreement; Altman 1991) and stimulus phases (Cohen's kappa = 0.95, excellent agreement). In cases of disagreement (N = 1 in the pre-stimulus and stimulus phase, respectively), the most conservative estimate was chosen; i.e., targets were recorded to look to the stimulus area in the pre-stimulus phase and not in the stimulus phase.

5.2.5 Statistics

The rationale for the choice of statistical analyses is detailed in Chapter 2, section 2.2.2.6. Repeated measures binomial logistic regressions (GLMM) were used for analyses of targets' looks to the stimulus area during the pre-stimulus and stimulus phases of experimental and control conditions, respectively, and to compare looks to the stimulus area during the stimulus phases of experimental and control conditions. Moreover, individuals' performance on the pre-stimulus and stimulus phases of the first trial received in individual conditions was analysed by means of non-parametric McNemar tests for repeated measures and nominal data. Null-hypotheses were rejected at an alpha level of 5%, and all tests were two-tailed.

5.3 Results

Bonobos followed the attention of conspecifics to the stimulus in 55.55% (12 of 22) of the time, 45.45% (5 of 11) and 63.64% (7 of 11), respectively, in *experimental* trials where they faced *towards* and *away* from the communicator at the start of stimulus projection (percentage is based on only the first trial that communicators received in the two experimental conditions). Communicators produced a visible behaviour while being in targets' 'open' or 'peripheral' field of vision (approached or touched the stimulus, shifted gaze between the stimulus and target, repositioned body while looking at stimulus, or arrested current behaviour) in 68.18% (15 of 22) of the first received experimental trials (facing *towards* and facing *away* from the communicator). Conspecifics followed the communicator's attention in 75% (3 of 4) of experimental trials where conditions were comparable to those, under which the intra-specific attention following of five other primate species have been tested (Tomasello *et al.* 1998); That is when (i) communicators

produced a visible cue while being in the target's 'open'/'peripheral' field of vision, (ii) targets faced *towards* the communicator at the start of stimulus projection, and (iii) targets were required to only 'turn' around (rather than 'locomote' around an obstacle) to look to the stimulus.

Comparisons within conditions (of pre-stimulus and stimulus phases - 'Pre versus post' control):

Bonobo targets were more likely to look to the stimulus area during the stimulus phase than pre-stimulus phase of experimental trials, including when the conditions where the target faced *towards* and *away* from the communicator at the start of the stimulus phase, respectively, were analysed separately ('*Experimental*' conditions collapsed: All trials received, GLMM: Est. = 3.65, SE = 1.09, z = 3.35, $p = 0.001$; '*Experimental-Towards*': All trials received: Est. = 3.93, SE = 1.41, z = 2.78, $p = 0.005$; Analysis of first trial, McNemar test: $\chi^2 = 4.05$, N = 11, $p = 0.044$; '*Experimental-Away*': All trial received: Est. = 3.82, SE = 1.01, z = 3.38, $p = 0.001$; Analysis of first trial, McNemar test: $\chi^2 = 10.23$, N = 11, $p = 0.001$).

In contrast, there was no significant difference in the likelihood of targets looking to the stimulus area during the pre-stimulus and stimulus phases of the control trials ('*No Stimulus-Towards*: All trials received, GLMM: Est. = 0.00, SE = 185700.00, z = 0, $p = 1$, Analysis of first trial, McNemar test: $\chi^2 = 0.03$, N = 11, $p = 0.871$; '*No Stimulus—Away*'': All trials received: Est. = 0.00, SE = 185700.00, z = 0, $p = 1$, Analysis of first trial: $\chi^2 = 0.03$, N = 11, $p = 0.871$; '*Target Alone/Target and Ignorant Communicator*': All trials received: Est. = 0.00, SE = 107200.00, z = 0, $p = 1$, Analysis of first trial: $\chi^2 = 0.02$, N = 11 $p = 0.880$[40], Figure 5.10, Table 5.4a).

Considering the duration of looks, targets overall oriented significantly longer towards the stimulus area (i.e., the stimulus fell within the targets' 'open' field of vision) during the stimulus phase (mean = 4.50s, s.d. = 2.68) than pre-stimulus phase (mean = 0.06, s.d. = 0.24) of all experimental trials (despite the stimulus being removed before targets could view it: repeated measures t-test conducted on trials, where targets looked to the stimulus area during either the pre-stimulus or stimulus phase: ($t(19) = -5.78$, $p < 0.000$).

[40] There was no significant difference between targets looking to the stimulus when displayed outside the view of a '*Target Alone*' and a '*Target and Ignorant Communicator*' (comparison of stimulus phases of the two conditions: N = 60, $p = 1$). Therefore, and since '*Target Alone*' trials for some subjects were substituted by the more conservative '*Target and Ignorant Communicator*' trials, the two conditions were collapsed.

Comparisons across conditions (of looks to the stimulus area during stimulus phases)

Targets were more likely to look to the stimulus area during the stimulus phase of experimental than control conditions (All trials received: GLMM with 'look/no-look' and '*Experimental*', '*No Stimulus*' and '*Target Alone*'/'*Target and Ignorant Communicator*' conditions entered as factors and participant as a random factor: '*Experimental*' vs. '*No Stimulus*': Est. = -3.18, SE = 1.01, z = 3.01, p = 0.001; '*Experimental*' vs. '*Target Alone*'/'*Target and Ignorant Communicator*': Est. = -3.12, SE = 1.17, z = 3.18, p = 0.001; Analysis of first trial: McNemar test: '*Experimental-Towards*' vs. '*No Stimulus-Towards*': χ^2 = 7.68, N =11, p = 0.006; "*Experimental-Away*' vs. '*No Stimulus-Away*': χ^2 = 10.23, N =11, p = 0.001, Figure 5.10, Table 5.4a).

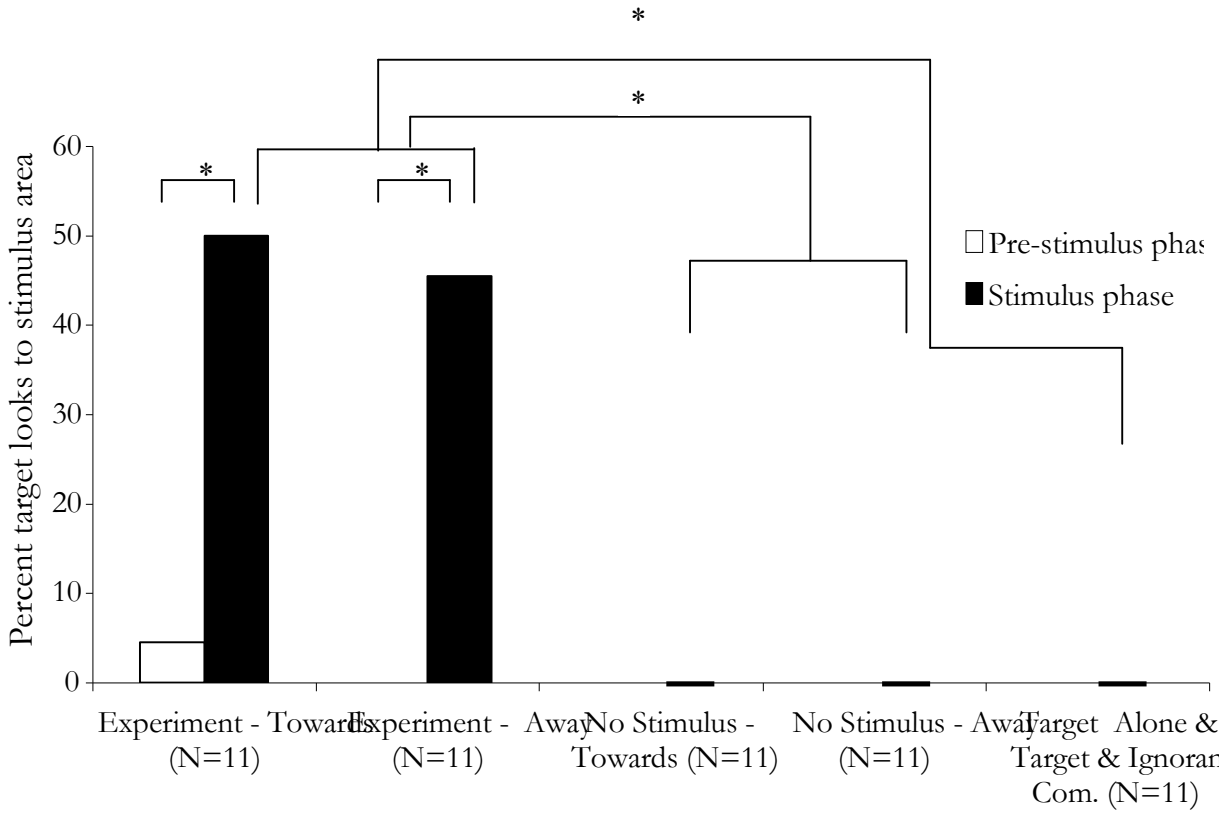


Figure 5.10: Target looks to the stimulus area. Percent target looks to the stimulus area during the pre-stimulus and stimulus phases of experimental and control conditions (based on the average response to all trials that individual subjects received). Asterisks indicate significant differences between target looks to the stimulus location during stimulus and stimulus phase of experimental trials, and during the stimulus phases of experimental and control trials.

Trials requiring targets to only turn around to look to the stimulus

Considering the subset of trials that required targets to only turn around so as to look to the stimulus (22% of all trials, 31of 139), bonobos looked to the stimulus in 80% (4 of 5) and 100% (2 of 2) of *experimental* trials where the target faced *towards* and *away* from the communicator at the start of stimulus projection, respectively. Targets were more likely to look to the stimulus area during the stimulus phase than pre-stimulus phase of *experimental* trials (GLMM: Estimate = 4.89, SE = 1.95, z = 2.51, $p = 0.012$), though this was not the case when trials where they faced *towards* and *away* from the communicator at the start of the stimulus projection were analysed separately, nor when any of the control trials were considered (GLMM, *'Experimental-Towards'*: Est. = 22.47, SE = 61.13, z = 0.37, $p = 0.71$; Analysis of first trial: McNemar test: $\chi^2 = 2.5$, n = 5, $p = 0.114$; '*Experimental-Away*': GLMM, Est. = 47.13, SE = 131010.68, z = 0, $p = 1$; Analysis of first trial: $\chi^2 = 2.25$, n = 2, $p = 0.134$; '*No Stimulus–Towards*': GLMM, Est. = 0.00, SE = 190400.00, z = 0, $p = 1$; Analysis of first trial: $\chi^2 = 0.10$, n = 5, $p = 0.751$; '*No Stimulus–Away*': Est. = 0.00, SE = 151900.00, z = 0, $p = 1$; Analysis of first trial: $\chi^2 = 0.06$, n = 9, $p = 0.814$; *'Target Alone'/'Target and Ignorant Communicator'*: Est. = 0.00, SE = 124700.00, z = 0, $p = 1$; Analysis of first trial: $\chi^2 = 0.13$, n = 5, $p = 0.752$).

There were no significant differences between targets' looks to the stimulus location across *experimental* and control trials ('*No Stimulus*': GLMM: Est. = -23.36, SE = 1135.94, z = 0, $p = 0.998$; *'Target Alone'/'Target and Ignorant Communicator'*: Est. = -23.36, SE = 1967.49, z = 0, $p = 0.999$, Table 5.4b).

Trials requiring targets to locomote around a barrier to look to the stimulus

Considering the subset of trials that required targets to first locomote around a visual barrier to look to the stimulus (78% of all trials, 108 of 139), there were no significant differences between targets' looks to the stimulus location during the pre-stimulus and stimulus phases of any of the conditions, nor across the stimulus phases of the various conditions when all trials that participants received were considered (see Table 5.4c and Figure 5.11).

Considering, however, only the first trial that participants received, targets were more likely to look to the stimulus location during the stimulus than pre-stimulus phase of experimental trials (McNemar test: '*Experimental-Towards*': $\chi^2 = 4.10$, n = 10, $p = 0.044$; '*Experimental-Away*': $\chi^2 = 6.05$, n = 10, $p = 0.014$). In contrast, there were no significant differences between target looks to the stimulus area during the pre-stimulus and stimulus phases any of the control trials ('*No Stimulus-Towards*': $\chi^2 = 0.03$, n = 10, $p = 0.871$; '*No Stimulus-Away*': $\chi^2 = 0.03$, n = 7, $p = 0.871$; '*Target Alone*'/'*Target and Ignorant Communicator*': $\chi^2 = 0.05$, n = 10, $p = 0.823$, Figure 5.11). Moreover, analysing the performance for the 6 subjects that received at least one '*Experimental-Towards*', '*Experimental-Away,* '*No Stimulus-Towards*' and '*No Stimulus-Away*' 'locomote' trial, targets were significantly more likely to look to the stimulus area during the stimulus location of *experimental* than '*No Stimulus*' trials (McNemar test of first trial received: $\chi^2 = 5.04$, n = 6, $p = 0.025$).

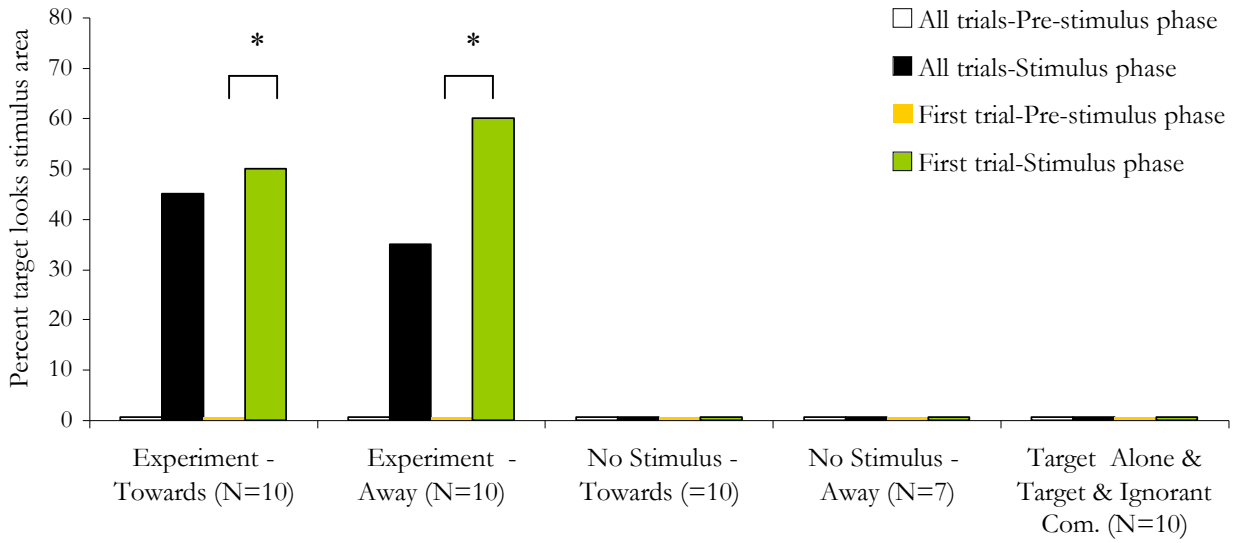


Figure 5.11: Locomote trials. Percent target looks to the stimulus area during the pre-stimulus and stimulus phases of experimental and control trials that required targets to first locomote around an obstacle (measure is based on the average response to all 'locomote trials that individuals subjects received). Asterisks indicate significant differences across the pre-stimulus and stimulus phases of experimental conditions based on analysis of the first received trial.

Table 5.4: Results summary. Statistics for all trials (Table a), and for the data-subsets where targets were required to either only 'turn' (Table b), or to 'locomote' around a barrier to look to the stimulus (Table c). The hypotheses predicted a difference between target looks to the stimulus locations in comparisons 1-3 and 7-8, and none in comparisons 4-6. Significant differences are highlighted in grey. Analysis of comparison c7 for first trial received was based on the performance of 6 subjects.

a) All trials		**All trials**					
Trial type(s) compared	**Intervals compared**	**GLMM**				**McNemar Test (first trial received)**	
		Estimate	**SE**	**z**	***P***	χ^2	***P***
1 Experimental (all trials)	Pre- & Stimulus	3.65	1.09	3.35	0.001		
2 Exp. - Target faces towards com.	Pre- & Stimulus	3.93	1.41	2.78	0.005	4.05	0.044
3 Exp. - Target faces away from com.	Pre- & Stimulus	3.82	1.01	3.38	0.001	10.23	0.001
4 No Stimulus - Target faces towards com.	Pre- & Stimulus	0.00	185700.00	0.00	1.000	0.03	0.871
5 No Stimulus - Target faces away from com.	Pre- & Stimulus	0.00	185700.00	0.00	1.000	0.03	0.871
6 Target Alone / Target & Ignorant com.	Pre- & Stimulus	0.00	107200.00	0.00	1.000	0.02	0.880
7 Exp. & No Stimulus	Stimulus	-3.18	1.01	3.01	0.001	9.82	0.002
8 Exp. & Target Alone/Target & Ign. com.	Stimulus	-3.12	1.17	3.18	0.001	19.11	0.000

b) 'Turn' trials		**Turn**					
Trial type(s) compared	**Intervals compared**	**GLMM**				**McNemar Test (first trial received)**	
		Estimate	**SE**	**z**	***P***	χ^2	***P***
1 Experimental (all trials)	Pre- & Stimulus	4.89	1.95	2.51	0.012		
2 Exp. - Target faces towards com.	Pre- & Stimulus	22.47	61.13	0.37	0.710	2.50	0.114
3 Exp. - Target faces away from com.	Pre- & Stimulus	47.13	131010.68	0.00	1.000	2.25	0.134
4 No Stimulus - Target faces towards com.	Pre- & Stimulus	0.00	190400.00	0.00	1.000	0.10	0.751
5 No Stimulus - Target faces away from com.	Pre- & Stimulus	0.00	151900.00	0.00	1.000	0.06	0.814
6 Target Alone / Target & Ignorant com.	Pre- & Stimulus	0.00	124700.00	0.00	1.000	0.13	0.752
7 Exp. & No Stimulus	Stimulus	-23.36	1135.94	0.00	0.998		
8 Exp. & Target Alone/Target & Ign. com.	Stimulus	-23.36	1967.49	0.00	0.999		

c) 'Locomote' trials		**Locmote**					
Trial type(s) compared	**Intervals compared**	**GLMM**				**McNemar Test (first trial received)**	
		Estimate	**SE**	**z**	***P***	χ^2	***P***
1 Experimental (all trials)	Pre- & Stimulus	19.18	3132.86	0.00	0.995		
2 Exp. - Target faces towards com.	Pre- & Stimulus	19.24	4262.83	0.00	0.996	4.10	0.044
3 Exp. - Target faces away from com.	Pre- & Stimulus	19.11	4179.00	0.00	0.996	6.05	0.014
4 No Stimulus - Target faces towards com.	Pre- & Stimulus	0.00	139700.00	0.00	1.000	0.03	0.871
5 No Stimulus - Target faces away from com.	Pre- & Stimulus	0.00	167900.00	0.00	1.000	0.03	0.871
6 Target Alone / Target & Ignorant com.	Pre- & Stimulus	0.00	130000.00	0.00	1.000	0.05	0.823
7 Exp. & No Stimulus	Stimulus	-20.19	6278.00	0.00	0.997	5.04	0.025
8 Exp. & Target Alone/Target & Ign. com.	Stimulus	-20.19	3974.00	0.00	0.996		

5.4 Discussion

The study aimed to assess the conspecific gaze-following skills of bonobos, who reliably followed the attention of conspecifics in a non-competitive context, to locations behind themselves. More specifically, bonobos were more likely to look to the area of a novel stimulus when in the presence of a conspecific who viewed the stimulus, than in the absence of a conspecific, or in the presence of a conspecific ignorant as to the stimulus, and when no stimulus was projected. Bonobos followed the attention of conspecifics in 46% of trials when facing a conspecific viewing the stimulus (compared to 60% for the chimpanzees tested, percentages based on the first trial received). Where conditions were comparable to those, where the intra-specific gaze following of chimpanzees, mangabeys and macaques has been tested (Tomasello *et al.* 1998), and only trials where the communicator produced a *visible* cue while in the target's 'open'/'peripheral' visual field were included (and targets were required to only 'turn' around to co-orient with communicator attention), bonobos and chimpanzees followed conspecific attention at comparative levels (bonobos: 75% of trials; chimpanzees: 64%, see Chapter 2, Chimpanzee Attention Following).

Like chimpanzees, bonobo targets oriented longer towards the stimulus area during the stimulus than pre-stimulus phase of experimental trials (although the stimulus was removed before it came within targets' view), suggesting an expectation of a point of interest. While it cannot be ruled out that targets might have peripherally detected a flicker of the stimulus, the analysis of looking duration supports the attention following interpretation.

When trials that required targets to only *turn* (rather than first '*locomote*' around a visual barrier) so as to co-orient to the communicator's attention, were analysed separately, targets were more likely to look to the stimulus area during the stimulus than pre-stimulus phase of experimental trials, although the difference between experimental and control trials was non-significant. As these analyses were performed post-hoc, the number of subjects who received experimental trials requiring targets to either 'turn' or first 'locomote' around a barrier to look to the stimulus varied, and the 'turn' trial sample size was too small to draw any meaningful conclusions from this analysis.

Bonobo targets followed conspecific attention under unfavourable geometric conditions that required them to first locomote around a visual barrier (when the first trial that subjects received were considered, however, these comparisons did not yield significant results when *all* of the trials that individuals received were considered, jointly). While previous research has

demonstrated that four bonobos with substantial experimental experience follow human gaze to distal locations, around opaque barriers and through windowed obstructions (Bräuer *et al.* 2005; Okamoto-Barth *et al.* 2007a), the present results represent the first evidence to show that, overall, geometric co-orientation to others' attention also occurs during interactions between conspecifics (and among experimentally naive bonobos). The results support the argument that bonobos do not simply respond automatically to the attention of others, but may have some understanding that attention signifies that another is somehow connected to an external target, and that the animals follow the attention of others around barriers in an apparent attempt to take their visual perspective. Thus, bonobos seem to be either naturally interested in the attention of conspecifics as reflected by adventitious cues (and motivated to locomote in order to co-orient thereto, possibly underscored by the species', seemingly overall, highly 'active' way of life), or the bonobo communicators produced highly salient and/or intentional cues, as to the focus of their attention.

While previous research suggests that bonobos have some understanding that what others see influence their behaviour and behave differently when recipients face towards and away from them (Kaminski *et al.* 2004; Liebal *et al.* 2004a), the present results suggest that bonobos consistently led non-attentive conspecifics to look to a novel stimulus suggesting that bonobos may possibly (like chimpanzees: Menzel 1973) direct conspecifics to hidden objects in a manner that elicits an attentional response. Ascertaining whether the bonobos led non-attending conspecifics to look to stimulus by means of adventitious or intentional behaviours, however, requires analysis of the communicators' behaviours. The next chapter explores whether particular behaviours produced by individuals viewing the stimulus consistently led to conspecific attention re-orientation, and if individuals intentionally redirected conspecifics' attention.

CHAPTER 6: Bonobo manipulation of conspecific attention

Summary

There have been no systematic tests on conspecific attention directing in bonobos, and virtually no data regarding this exists, except for anecdotal observations of one wild individual and two language-trained bonobos. This chapter aimed to identify behaviours that may act as cues triggering attention following in bonobos, and test the hypothesis that bonobos have the ability and motivation to direct conspecifics to a novel stimulus. The behaviour of the 11 bonobos who were presented with a novel stimulus while alone or in the presence of an attentive or non-attentive conspecific (see Chapter 5) was examined. Bonobos were significantly more likely to produce a stimulus directional cue when they viewed the stimulus in the presence of an initially non-attentive conspecific, though the behaviour did not significantly predict conspecifics' looks to the stimulus area. There was no significant difference in the distribution of auditory and multi-modal behaviours (sequential auditory and stimulus directional behaviours) across the three conditions, though individual differences were evident, and all auditory behaviours were followed by stimulus directional behaviours, and all in contexts, in which the animals viewed the stimulus in the presence of a non-attentive conspecific. There were no significant differences in the distribution of locomotory, visual non-stimulus directional across the three conditions, and no indication that the bonobos intentionally used gaze as a communicative referential signal. Overall the results do not lend support to the predictions of the 'Emotional Reactivity Hypothesis' (Hare & Tomasello 2005), which suggests that the bonobos might outperform the chimpanzees.

6.1 Introduction

Bonobo auditory gestures

Two of the most debated topics with respect to nonhuman primate use of gestures, facial expressions, and vocalisations are whether they are used intentionally and referentially, or are simply side effects of responses to external events, driven mainly by arousal and emotional states (see Chapter 1 and Tomasello & Call 1997). As many other primates, bonobos respond to external events with vocal signals that frequently attract other group members and provide referential information about the events (bonobos: Clay & Zuberbühler 2009; chimpanzees: Slocombe & Zuberbühler 2005, 2006; rhesus macaques: Hauser & Marler 1993a,b; toque macaques: Dittus 1984). Indeed, bonobos call more frequently when they discover food in the presence of conspecifics (Van Krunkelsven *et al.* 1996), and produce acoustically distinct call types in response to differentially preferred food items, which listeners may use to draw inferences about the items (Clay & Zuberbühler 2009). Bonobos thus use vocalisations in seemingly complex ways, and field researchers have noted a near incessant cacophony of sound in bonobo parties (Bermejo & Omedes 1999), and emphasized the importance of the 'peep' and other close contact calls in within-party communication. Following a study of the communicative repertoire of 10 captive bonobos, de Waal suggested that their most common vocalisation, the soft 'food peep', functions "to draw attention to and 'comment' on objects, food, and events in the environment" (de Waal 1988, p. 211), a key characteristic of early human language development and language in general (Tomasello & Carpenter 2007). The observational nature of de Waal's study, however, raises questions as to the validity of concluding that 'food peeps' actually carry the *referential function* suggested. Nonetheless, despite flexibility within their vocal communication system, bonobo vocalisations display less flexibility than their gestures (Pollick & de Waal 2007), most likely because vocalisations are closely tied to specific emotions, such as fear, aggression and affiliation (Tomasello & Call 1997; Corballis 2002; Call & Tomasello 2007). The question thus remains, whether such vocalisations are intentionally communicative acts emitted to inform others, or relatively inflexible responses to external events, that reflect merely arousal changes in the signaller (or indeed some combination of the two). A promising candidate for intentionally acoustic communicative signals are so-called 'auditory gestures' (see e.g., Tomasello & Call 1997), such as clapping or banging on objects, which may allow bonobos to produce auditory signals with higher flexibility than is feasible given their vocal system.

Bonobo visual gestures

Compared to vocalisations, gestures are an evolutionarily more recent arrival, as suggested by their complexity in the Hominoids and comparatively limited presence in monkeys (Tomasello & Call 1997; Corballis 2002; Call & Tomasello 2007). Moreover, gestures are less closely linked to specific emotions and therefore subject to greater cortical control than vocalisations (e.g., Wiesendanger 1999), and both *Pan* species use communicative gestures more flexibly than vocalisations and facial expressions (Pollick & de Waal 2008). Relatively little is known about the gestural communication of wild bonobos, although some studies have devoted attention to gestures (e.g., Kano 1992; Ingmanson 1996; Veà & Sabater-Pi 1998). The most systematically collected data stem from observational studies of captive bonobos, and their interactions with human experimenters, which suggest that bonobos have similar sized repertoires to chimpanzees, consisting of 20-30 gestures (Savage-Rumbaugh *et al.* 1977; de Waal 1988; Pika *et al.* 2005). In addition, bonobos frequently use the species-typical behaviour, peering (prolonged gazing within 30 cm of a conspecific's face), which although used in many contexts, has been suggested to function to solicit interactions (Idani 1995, cited by Johnson *et al.* 1999).[41]

Bonobo attention solicitation and directing

Systematic observations suggest that, while bonobos beg food from one another and infants may include objects in social play, they engage in very few triadic interactions with conspecifics around objects (Bard & Vauclair 1984; Tomonaga *et al.* 2004). In contrast, adult bonobos have been shown to engage in some degree of coordinated attention with both humans and conspecifics, by repeatedly alternating gaze between a novel object and a human or conspecific (Pitman & Shumaker 2009). Bonobos who are reared with human contact and have been explicitly or implicitly exposed to the functional aspects of human pointing may, furthermore, direct humans to things that they want and directions they wish to travel (by means of e.g., an out-stretched arm and hand: Savage-Rumbaugh 1986, 1998). As most intra-specific gestures (de Waal 1988), such gestures are, however, of an imperative nature and about spurring others into action to do something for the subject.

[41] 'Peering' is described as a highly stereotyped social interaction, where the 'peerer' approaches and positions its face often within centimetres of a conspecific's. The behaviour is primarily performed by younger animals to more dominant females, and given its production in inter-group encounters, where it eases tensions (Idani 1995, cited by Johnson *et al.* 1999), its function is suggested to be one of initiating amicable interactions.

While bonobos have some understanding that what others see influences their behaviour, and adjust their food begging behaviour to the attentional state of cooperative human experimenters by locomoting to places where their gestures can be seen (Kaminski *et al.* 2004), there is little evidence that they follow auditory attention calling signals with more specific, visual gestures. For example, when faced with desirable, out-of-reach food and a human experimenter facing away from the subject, bonobos tend to locomote, so as to gesture towards the food in front of the non-attentive experimenter, rather than first call the experimenter's attention (Liebal *et al.* 2004a). Interestingly, however, the picture becomes more complex when contexts more dynamic than the rather formalised food-begging situation are considered. In contrast to chimpanzees (Warneken & Tomasello 2006), young bonobos actively encourage reluctant human partners to re-engage in social games by means of intentional gestures, accompanied by eye contact and/or response waiting (Pika & Zuberbühler 2008). This behaviour has been interpreted as evidence of some form of shared intentionality (Pika & Zuberbühler 2008), in which interlocutors engage in collaborative interactions and share psychological states with one another (Bratman 1992; Gilbert 1992, cited by Tomasello & Carpenter 2007). The absence of this form of collective intentionality has previously been suggested to underlie the lack of declarative signalling in non-human species (Tomasello 2007; Tomasello & Carpenter 2007).

While de Waal (2001) has suggested that bonobos may use gaze as an intentional referential signal, in lieu of imperative manual pointing (by engaging in ostensive behaviour and alternating gaze between the interlocutor and a desired object) there is little evidence that (non-language trained) bonobos point for and show things to one another (e.g., Bard & Vauclair 1984). Long-term field studies of bonobos, spanning over 40 years, have not identified referential pointing as a frequent element in their communicative repertoires. The only documented instance of pointing by wild bonobos stems from one individual observed to extend an outstretched arm towards some poorly hidden nearby scientists, while vocalising and alternating gaze between the humans and its conspecifics, repeating the pointing sequence twice (Veà & Sabater-Pi 1999).

Reports of inter-specific declarative-like signalling stem from human-raised and language-trained bonobos who have been observed to direct the attention of human caretakers to unusual sounds by means directional looking and gesturing (Savage-Rumbaugh *et al.* 1986, 1998)[42]. Importantly, all these reports are anecdotal and without exception lack proper controls; in all cases interpretation is at issue. Indeed, an interesting observation that bonobos may use iconic

[42] "When she [Matata] heard unusual sounds in the forest, she would direct my attention towards them by looking and gesturing in that direction" (Savage-Rumbaugh *et al.* 1998, p. 11).

gestures (i.e., gestures that depict motion in space, such as a male bonobo moving a hand across a female's body to indicate the action or position he wanted her to take: Savage-Rumbaugh *et al.* 1977), has not been replicated in a systematic follow-up study of 20 other bonobos from three different populations (Roth 1995). Zimmermann and colleagues (Zimmermann *et al.* 2009) found that five bonobos used fingers protruded through metal mesh or Plexiglas holes to guide a human experimenter to the location of a hidden tool needed to retrieve food for the bonobo, suggesting an ability to adjust communication in accordance to the human's knowledge of the tool location, and point to the location when needed. While it remains unresolved if the pointing in the experiment was motivated by an intention to inform the human about the tool's location (informative pointing) or represented a complex imperative request that the human recover and use to tool to retrieve food (Gómez 2004; Zimmermann *et al.* 2009), the principle of parsimony and general paucity of reported instances of informative pointing in bonobos tilts the interpretation towards a complex imperative request.

An experimental study involving non-language trained bonobos interacting with conspecifics, suggest that, in contrast to chimpanzees, bonobos are motivated to cooperate to procure and share food, even when there is no immediate benefit to themselves (Hare *et al.* 2007; Hare & Kwetuenda 2010). Thus, if the paucity of ape pointing is due to motivational rather than cognitive factors, and the rarity with which relevant situations present themselves (Leavens *et al.* 1996), the question arises whether bonobos may be more likely than chimpanzees to actively lead conspecifics to view a novel stimulus.

While the 'Emotional Reactivity Hypothesis' (Hare & Tomasello 2005) suggests that chimpanzees are unable to overcome their social intolerance and competition in foraging contexts, this does not necessarily imply a *Pan* species difference in motivation to share attention to novel, non-food objects. Indeed, a recent finding that bonobos (Hare, unpublished data), as chimpanzees (Hare & Tomasello 2004), are also not able and/or inclined to use the human pointing gesture to locate hidden food in a cooperative object-choice task, raises doubt as to whether chimpanzees' poor performance on the task stem solely from its collaborative nature. The explanation for these contrasting data may lie in a combination of food incentives and the inter-specific communicative setting of the object-choice task; i.e., that chimpanzees' social intolerance prevents intra- as inter-specific cooperation in foraging contexts, and that both species fail in cooperative inter-specific interactions. Alternatively, a recent finding that bonobos, chimpanzees and orangutans, with extensive experience with the object-choice task perform better when experimenters perform highly distal rather than more proximal points

(100cm vs. 40cm distance to an indicated container) has led to the suggestion that apes' typically poor performance on the object-choice task rests on methodological rather than cognitive / motivational factors (Mulcahy & Call 2009; Lyn 2010). The question, however, remains whether the *Pan* species exhibit different motivations in the manipulation of conspecific attention, and if bonobos may be more likely to lead conspecifics to view a novel stimulus.

Aims of the study

This study aimed to explore if bonobos who view a novel stimulus, consistently behave in ways that may act as cues triggering intra-specific attention following, and test the hypothesis that the species has the ability and motivation to direct conspecifics to a novel stimulus and engage in referential signalling other than necessarily hand-pointing. This study is particularly significant, as there have been no systematic tests on conspecific attention directing in bonobos, and virtually no data regarding this exists, except for the anecdotal observations of one wild individual and of language-trained bonobos.

To test if communicators actively called the attention of non-attentive conspecifics, and led them to look to the stimulus that only they observed, it was (as in Chapter 3: Chimpanzee Manipulation of Conspecific Attention) recorded whether communicators produced different behaviours or combinations thereof when: (1) in the presence of the stimulus but absence of a conspecific ('*Communicator Alone*'), and in the presence of the stimulus and an (2) attentive or (3) non-attentive conspecific (social and non-social *Experimental* conditions). As in Chapter 3, it was predicted that communicators would behave differently as a function of conspecific's presence and visual attention. Specifically, it was predicted that there would be:

(i) A difference in the frequency of auditory behaviours produced across the conditions, and a difference in the likelihood that non-attentive conspecifics looked to the stimulus area when communicators produced an auditory behaviour.

(ii) A difference in the frequency of visual stimulus directional behaviours when in the presence of the stimulus, and either in the presence or absence of a conspecific, and a difference in the likelihood conspecifics looking to the stimulus area when communicators produced stimulus directional behaviours.

(iii) No difference in the frequency of visual non-stimulus directional behaviours in *experimental* and '*Communicator Alone*' conditions; nor in the likelihood of conspecifics looking to the

stimulus area when communicators produced non-stimulus directional behaviours in *experimental* conditions.

The chapter examines de Waal's (2001) suggestion that bonobos may use gaze as an intentional referential signal by examining communicators' gaze behaviour after looking to the stimulus, and target conspecifics' responses thereto. It was predicted that:

(iv) When within a conspecific's 'open' or 'peripheral' field of vision (see Figure 2.15), communicators would be more likely than chance to look to the conspecific within 2s of looking away from the stimulus, followed by a look to the stimulus within 2s of looking away from the conspecific (gaze behaviour: stimulus-target-stimulus). Due to the difficulty of distinguishing such behaviour from referential looking, specific attention was paid to trials, where communicators preceded the gaze behaviour with an auditory signal. Thus, the hypothesis that bonobos might use gaze as a communicative behaviour would be supported if targets were more likely to look to the stimulus location when communicators produced an auditory behaviour, followed by stimulus-target-stimulus gaze behaviours while being within the targets 'open'/'peripheral' field of vision.

(v) There would be a difference in the likelihood of conspecifics looking to the stimulus area when communicators produced the above behaviour.

6.2 Methods

6.2.1 Design

The analyses were based on the experiment described in Chapter 5, involving 11 bonobos. The comparisons involved the *experimental* and '*Communicator Alone*' conditions, designed to test if behaviours produced by bonobos who viewed a novel stimulus while alone, or in the presence of an attentive, or non-attentive conspecific, reflected a heightened state of arousal or possessed a communicative function, i.e., if communicators took conspecific presence and attentional state into account. Seventy-three percent of participants (N = 11) received a '*Communicator Alone*' trial before the first *experimental* trial (see Figure 5.3).

6.2.2 Coding of Communicator Behaviour

The coding of communicators' behaviour followed the scheme devised for chimpanzees (see section 3.2.2 and Table 3.1) and were: (1) auditory behaviours (vocalise, clap, audibly move object), (2) visual non-stimulus directional behaviours (arrest current behaviour, move head back rapidly), (3) visual stimulus directional behaviours (touch, lean torso towards, move extremity or head in the direction of the stimulus), (4) locomotory stimulus directional behaviour (approach), (5) conspecific directed behaviours (looks to the conspecific that were preceded within 2s of a look to the stimulus, and instances where communicators produced an auditory behaviour and subsequently shifted gaze from the stimulus to the conspecific and back to the stimulus), (6) 'hunching' behaviour. Auditory cues were recorded by two camcorders (i.e., not by a separate microphone), and where necessary due to e.g., windy conditions and the animals' distance to the cameras, verbal comments were made (to the camcorders) and later transcribed.

6.2.3 Scoring and reliability

Two additional coders coded 34.48% (20 of 58) of *experimental* and '*Communicator Alone*' trials to assess inter-observer reliability in terms of communicator production of (1) auditory and (2) visual and (3) locomotory stimulus directional cues.[43] Inter-observer reliability with respect to visual and locomotory stimulus directional cues was perfect (Cohen's kappa = 1, n = 20), while it was good with respect to auditory cues (Cohen's kappa = 0.77, n = 20).

6.2.4 Statistics

As in Chapter 3, gaze behaviours were analysed by means of binomial tests, and the distribution of cues across conditions, and of communicators' cue production (and targets' look to the stimulus area when communicators produced particular cues), were analysed by means of binomial logistic regressions (GLMM, fitted by the Laplace approximation) with a binomial error structure.

[43] Trials were randomly selected for inter-observer reliability coding, except for trials that I had recorded as containing auditory cues, which were all included.

6.3 Results

6.3.1 Communicator behaviour

Communicators were more likely to produce a **visual stimulus directional behaviour** when they viewed the stimulus in the presence of a non-attentive than an attentive conspecific, or alone (see Table 6.1 for results of GLMM analyses). Forty-six percent (5 of 11) of bonobos produced stimulus directional behaviours during a larger proportion of *experimental* than '*Communicator Alone*' trials, while only one individual produced stimulus directional cues during a larger proportion of '*Communicator Alone*' trials (Figure 6.1). There were, however, no significant different in the production of stimulus directional behaviour across social and non-social conditions. Likewise, forty-six percent (5 of 11) of bonobo communicators produced stimulus directed behaviours during a larger proportion of '*Experimental-Away*' than '*Experimental-Towards*' trials, while only one individual produced stimulus directed behaviours during a larger proportion of '*Experimental-Towards*' trials (Figure 6.2). No 'hunching' postures were observed in any trials. There was no statistically significant difference in the production of and **visual non-stimulus directional behaviours** across the three conditions, although significance was approached for when communicators viewed the stimulus in the presence of a non-attentive conspecific, and in social rather than non-social conditions.

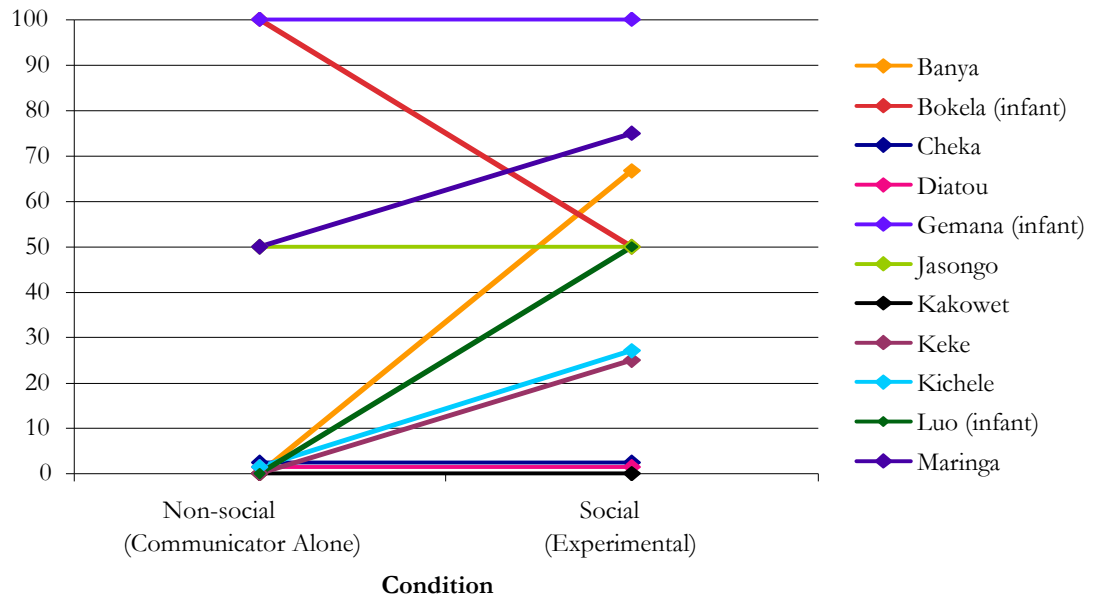


Figure 6.1: Visual stimulus directional behaviours. Percentage of trials where bonobo communicators produced visual stimulus directional behaviours in non-social ('*Communicator Alone*') and social (*experimental*, *facing towards/away*) conditions.

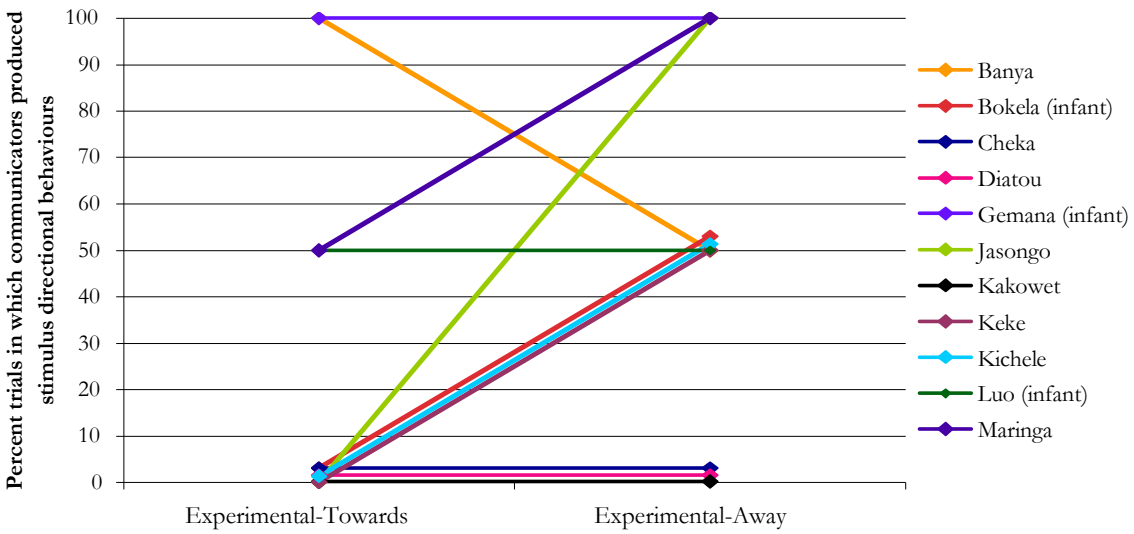


Figure 6.2: Production of visual stimulus directional behaviours in experimental conditions. Percentage of '*Experimental-Towards*' and '*Experimental-Away'* trials where bonobo communicators produced visual stimulus directional behaviours.

There were no significant differences in the communicators' production of **locomotory stimulus directional**, **auditory** and **multimodal behaviours** (sequential auditory and stimulus directional behaviours) across the three conditions, nor across social and non-social conditions. Bonobos, nonetheless, only produced auditory and multimodal behaviours when they viewed the stimulus in the presence of a non-attentive conspecific ('*Experimental-Away*': 20% of trials, N = 20; '*Experimental-Towards*': 0% of trials, N = 19; '*Communicator Alone*': 0% of trials, N = 19, Figure 6.3). All recorded auditory behaviours (N = 3) were followed by a stimulus directional behaviour.

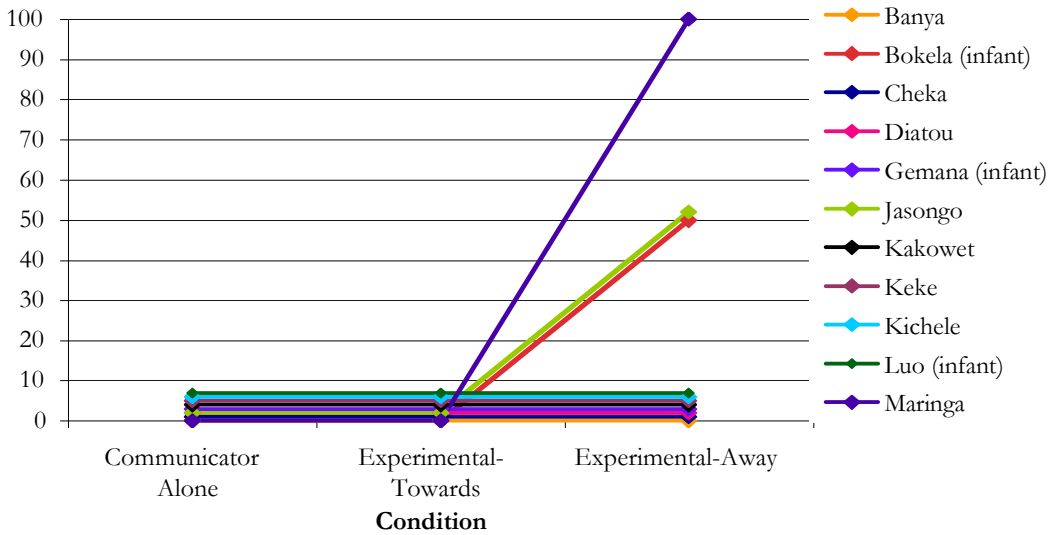


Figure 6.3: Auditory behaviours. Percentage of trials where individual bonobos produced auditory behaviours in '*Communicator Alone*', '*Experimental-Towards*' and *'Experimental-Away'* conditions.

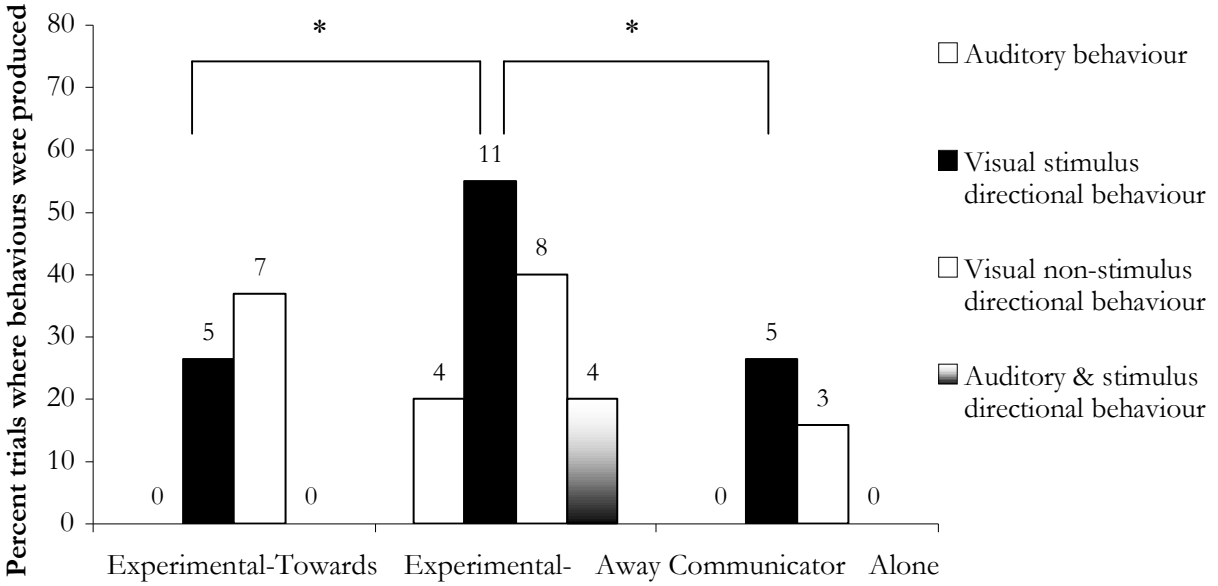


Figure 6.4: Behaviours produced across conditions. Percentage of '*Experimental-Towards*' (N = 19), '*Experimental-Away*' (N = 20), and '*Communicator Alone*' (N = 19) trials, where communicators produced various behaviours. Asterisks indicate significant differences across conditions.

Table 6.1: Results for GLMM analyses of the distribution of communicator behaviours across the '*Communicator Alone*', '*Experimental-Away*' and '*Experimental-Towards*' conditions. Significant and near-significant factors are highlighted in grey.

Behaviour	Model	Fixed effects	Estimate	Std. Error	z-value	*P*
Stimulus directional	1	Communciator Alone	0.61	0.68	0.51	0.590
		Experimental-Away	1.98	0.85	2.32	0.002
		Experimental-Towards	0.32	0.89	0.10	0.990
	2	Non-social	-1.50	0.77	0.95	0.509
		Social	1.00	0.70	1.41	0.158
Locomotory directional	3	Communciator Alone	-1.41	0.73	0.67	0.421
		Experimental-Away	0.60	0.79	0.76	0.448
		Experimental-Towards	0.40	0.81	0.50	0.621
	4	Non-social	-1.31	0.73	1.20	0.809
		Social	0.50	0.70	0.72	0.471
Non-stimulus directional	5	Communciator Alone	1.34	0.63	0.77	0.456
		Experimental-Away	1.33	0.78	1.72	0.086
		Experimental-Towards	1.20	0.79	1.52	0.128
	6	Non-social	-1.34	0.63	1.45	0.673
		Social	1.26	0.71	1.79	0.070
Auditory	7	Communciator Alone	-2.09	7.20	0.00	1.000
		Experimental-Away	1.92	5.05	0.72	0.451
		Experimental-Towards	-2.09	7.20	0.00	1.000
	8	Non-social	-19.64	4020.00	0.00	0.996
		Social	17.57	6.43	0.00	0.982
Multimodal	9	Communciator Alone	-2.09	7.20	0.00	1.000
		Experimental-Away	2.87	1.68	0.72	0.451
		Experimental-Towards	-2.09	7.20	0.00	1.000
	10	Non-social	-19.64	3593.61	0.00	0.996
		Social	17.06	6.43	0.00	0.982

Descriptions of trials containing auditory cues

Auditory and multimodal behaviours only occurred in four trials. While all recorded auditory behaviours met the requirement for inclusion in the auditory behaviour category, the underlying intentionality of auditory cue production was questionable in (at least) one trial (see Figure 6.8). Trials containing auditory behaviours are therefore described below:

1) Communicator viewed the stimulus and grunted. Target (female with infant) approached the stimulus area (on the right side of a tree, Figure 6.5). When the target was 2m from the communicator, the communicator looked to the target, approached and touched the stimulus, and then looked back to the target. Target approached and touched stimulus area.

Figure 6.5: '*Experimental-Away*' trial. Auditory (vocal) and stimulus directional behaviours.

2) Target left the outside area (entered an inside enclosure, and sat in the door immediately behind the plastic cover, Figure 6.6) and 30s pre-stimulus phase began. Communicator viewed the stimulus and clapped. Target returned, sat down and looked to communicator and stimulus area. Five seconds later communicator looked in the direction of the stimulus area and looked back to the target conspecific.

Figure 6.6: '*Experimental–Away*' trial. Auditory (clapping) and stimulus directional behaviours.

3) Infant communicator viewed, approached and touched the stimulus; vocalised quietly (grunted) and touched stimulus again (Figure 6.7). Target turned around and walked past communicator, and the communicator looked to the target and back to the stimulus.

Figure 6.7: '*Experimental–Away*' trial. Auditory (vocal) and stimulus directional behaviours.

4) Communicator viewed the stimulus displayed on the right hand side of a plastic bucket (Figure 6.8), approached and manipulated the bucket (lifted it and looked inside) and looked to conspecific. The target looked to the communicator and bucket, but did not approach and locomote around the bucket to look the stimulus.

Figure 6.8: '*Experimental–Away*' trial. Auditory (object manipulation) and stimulus directional behaviour.

Conspecific directed cues: Seventy-two percent (28 of 39) of *experimental* trials could be reliably scored for gaze changes. Of these, communicators were no more likely than chance to shift gaze from the stimulus to the conspecific and back to the stimulus while being within the conspecific's 'open'/'peripheral' field of vision (50 % [14 of 28] of trials, Binomial test: n = 28, $p = 0.572$). Communicators produced an auditory cue in 4 of 39 *experimental* trials, of which gaze behaviour could be reliably scored in three trials. In all three trials, communicators looked to the target conspecific within 2s of looking away from the stimulus, and in one case a communicator followed an auditory cue with 'stimulus-target-stimulus' gaze behaviour, while being within the conspecific's 'open'/'peripheral' field of vision.

During one '*Communicator Alone*' trial, a juvenile female communicator (who had previously viewed the stimulus in one '*Communicator Alone*' and four *experimental* trials (see Figures 6.6 and 6.8), approached and touched the stimulus, then approached and looked (for 2s) through a trapdoor to an inside enclosure containing conspecifics, after which she returned and re-engaged with the stimulus (Figure 6.9). No sound was heard from the inside enclosure.

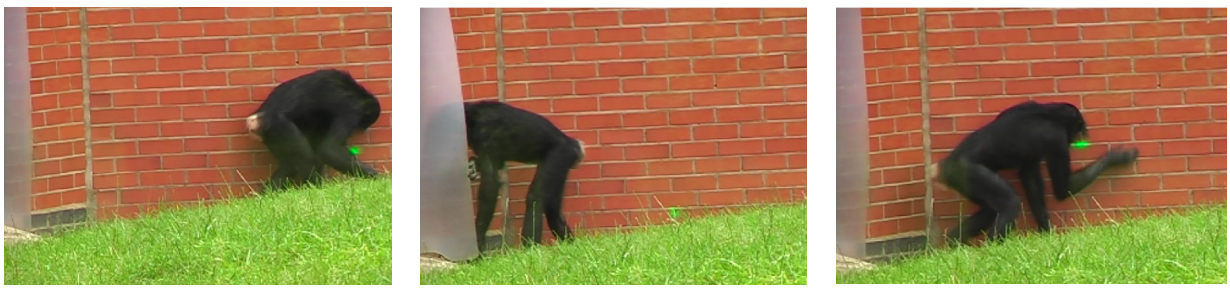


Figure 6.9: '*Communicator Alone*' trial.

6.3.2 Communicator behaviours leading targets to look to the stimulus area

None of the individually recorded behaviours that communicators produced significantly affected whether or not targets looked to the stimulus area during *experimental* trials (Table 6.2). Nor did the production of the compound category, 'multimodal behaviours', affect the probability of conspecifics looking to the stimulus area (GLMM, Est. = 1.27, SE = 1.20, z = 1.06 p = 0.291).

Table 6.2: Significance table. GLMM test for a difference in the probability that targets looked to the stimulus area when communicators produced various behaviours while viewing the stimulus in the presence of a conspecific (*experimental* conditions).

	Estimate	**Std. Error**	**Z-value**	***P***
Intercept	-1.10	0.52	2.12	0.034
Stimulus directional	0.68	1.10	0.62	0.538
Locomotory stimulus directional	0.00	1.43	0.00	0.999
Non-stimulus directional	1.60	1.23	1.30	0.192
Auditory	0.80	0.90	0.89	0.374

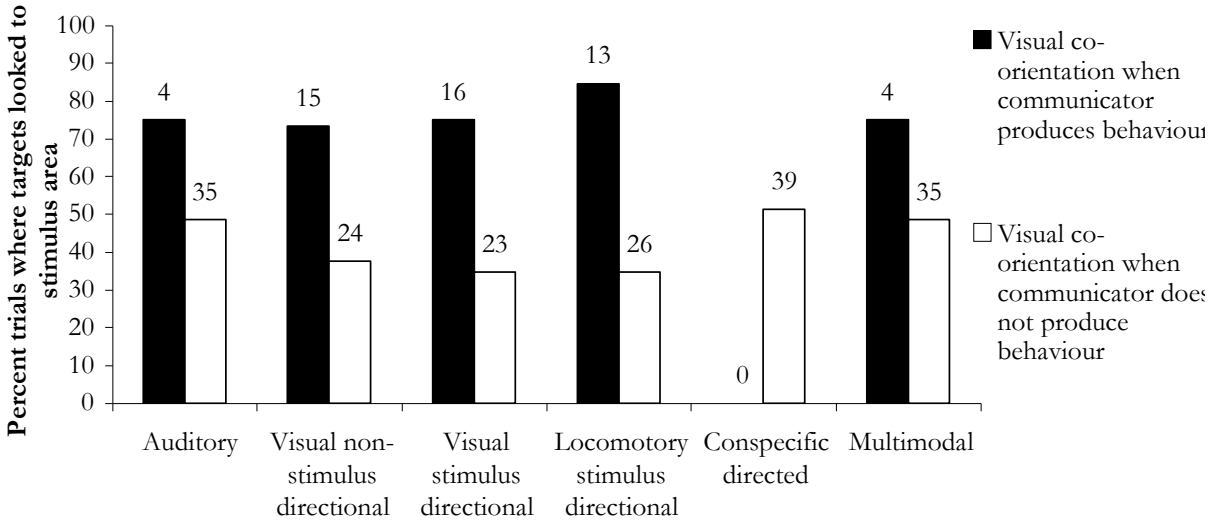


Figure 6.10: Target looks to stimulus area as a function of communicator behaviour. Percentage of targets' looks to the stimulus area during *experimental* trials (N = 39) when communicators did/did not produce various behaviours. Labels above columns indicate the number of trials in which communicators did and did not produce the behaviour.

6.4 Discussion

Did the bonobos preferentially produce stimulus directional behaviours when viewing the stimulus in the presence of conspecifics?

Contrary to prediction, the bonobos were no more likely to produce a visual stimulus directional behaviour when they viewed the novel stimulus in the presence of a conspecific than alone. Intriguingly (and like the chimpanzees tested under the same paradigm), the bonobos were, however, more likely to produce a stimulus directional behaviour they viewed the stimulus in the presence of a *non*-attending conspecific. While analyses of chimpanzee behaviour under the same paradigm suggest the some individuals may engage in intra-specific pointing by means of multi-faceted cues, such as the 'hunching' behaviour, no 'hunching' postures were observed in the bonobos.

Do bonobos preferentially produce auditory and multimodal behaviours when viewing the stimulus in the presence of a non-attentive conspecific?

The bonobos produced an auditory behaviour in only four trials, which were, however, all were followed by a stimulus directional behaviour, and all in contexts, in which the animals viewed the stimulus in the presence of a non-attentive conspecific. Coupled with the complete lack of auditory cues, and sequential auditory and stimulus directional cues in conditions where individuals viewed the stimulus alone or in the presence of an attentive conspecific it suggests some awareness and monitoring of conspecific attention, and sensitivity to their ability to receive the cues that the bonobos themselves produced. Nonetheless, as a group the bonobos were no more likely than chance to produce auditory or multimodal behaviours in the context of non-attentive conspecifics, and neither of these behavioural classes significantly affected conspecifics looks to the stimulus area. Indeed, contrary to prediction, none of the recorded behaviours that communicators produced increased the probability that conspecifics might look to the stimulus area. Any general conclusions regarding the behaviour of the animals that produced sequential auditory-stimulus-directional behaviours must therefore be prefaced with the caution that the selective production of the behaviours in the presence of a non-attentive conspecific failed to yield statistical significance at a group-wide level.

Do bonobos use gaze as an intentional referential signal?

Bonobos looked to conspecifics within two seconds of looking away from the stimulus in fifty percent (N=28) of experimental trials that could be reliably scored for gaze changes, which did, however, not deviate from chance. The trend is, nonetheless, consistent with a finding that three bonobos looked referentially to a conspecific upon viewing a human hold up an object (Pitman & Shumaker 2009), and with the first of the two defining criteria of social referencing, of (i) looking referentially between an object and another individual in order to subsequently (ii) regulate behaviour based on the emotional information received.

As with most ape studies (and the chimpanzee study reported in Chapters 2 and 3) there were noticeable individual differences, with for example, one adolescent female producing auditory and directional cues in all trials when viewing the stimulus in the presence of a non-attentive conspecific, and no auditory cues when alone or in the presence of a toward-facing individual. While viewing the stimulus in the presence of a non-attentive conspecific, the individual clapped and, upon attentional contact with a conspecific, looked to the stimulus location and back to the conspecific. In another trial the individual audibly manipulated a box, upon which the stimulus was shown, and seemingly alternated gaze between the box and the conspecific, once the conspecific turned around.[44] In one '*Communicator Alone*' trial the individual engaged with the stimulus, then approached and partly entered a trapdoor to an inside enclosure containing conspecifics, after which she returned and re-engaged with the stimulus. While it is possible that the animal responded to sounds from the inside enclosure, none were audible, and the behaviour is consistent with some form of referential looking that may have had the effect of either reducing stimulus induced arousal, or functioned to establish attentional contact with conspecifics for potential subsequent, adventitious stimulus detection.

To examine de Waal's (2001) suggestion that bonobos may intentionally use gaze as an intentionally communicative referential signal, and to separate such instances from mere referential looking I examined the bonobos gaze behaviour in the few trials, in which they produced an auditory cue, and which could be reliably scored for gaze behaviour. While the bonobos followed all auditory behaviours (N=4) with a look to a conspecific, they were no more likely than chance to precede gaze alternation (while being within the conspecific's 'open' or 'peripheral' field of vision) by an auditory behaviour, nor did this behaviour influence the

[44] Gaze behaviour could, however, not be unambiguously ascertained in this trial, and the trial was thus excluded from the gaze analysis.

probability that conspecifics looked to the stimulus. Thus, while there is some suggestion and evidence that apes may use gaze as an ostensive signal (Menzel 1973, 1974; O'Connell 1994; Gómez 1996; Veà & Sabater-Pi 1998; de Waal 2001) to direct other's attention to e.g., desired, objects or goals, the current results (partially due to the very small sample size) cannot lend support to the suggestion that bonobos use gaze and gaze alternation as referential signals to communicative about a distal object or event.

Conclusion

The cognitive sophistication underlying the bonobo behaviours remain obscure, as the design does not allow for a distinction between intentional attention calling and re-direction, and the possibility that individual arousal levels may be influenced by the mere presence of a toward-facing conspecific. The design does also not address the question of whether the apes behaved to influence others' mental states or to evoke an attentional and/or emotional reaction as reflected in overt manifestations. In the light of past research, however, it seems reasonable to conclude that (like chimpanzees) some bonobos, under some circumstances, may direct conspecifics to hidden objects to elicit an attentional response as reflected in overt manifestations (see Gómez *et al.* 1993). Some of the apes may have performed a form of simple showing, not unlike the earlier types of proto-declarative communication that human infants engage in, before they begin to point declaratively (Bates *et al.* 1975) and possibly some form of interrogative social referential pointing, to provoke a response that can be used to discern ambiguity in situations of uncertainty and provide information about an situation and how to respond.

Overall, the results do not support predictions of the 'Emotional Reactivity' Hypothesis (Hare & Tomasello 2005), that the socially more tolerant bonobos (Hare *et al.* 2007) should outperform the chimpanzees (Chapter 3). The 'Emotional Reactivity Hypothesis' is, however, predicated upon cooperation involving food, which may be predicted to evoke a higher degree of self-interest than an ambiguous, novel object. The behaviour of the individuals of the two species may be more comparable when presented with a stimulus predicted to evoke interest rather than want (or indeed, fear), than a monopolisable food object. For both the bonobos and chimpanzees, some individuals preceded directional gestures by an auditory signal in trials only where they viewed the stimulus in the presence of a non-attentive conspecific, and consistently led conspecifics to the stimulus. Thus, for both species there were noticeable individual differences, urging caution in deriving species-wide conclusions on the basis of tests involving limited sample sizes.

CHAPTER 7: Attention following in orangutans

Summary

Research suggests that orangutans are sensitive to the attentional states of others and follow the gaze of humans. This study investigated whether orangutans follow the attention of conspecifics, and presented seven Bornean orangutans (*Pongo pygmaeus pygmaeus*) with a novel visual stimulus to test if conspecifics would detect it under two experimental conditions. In one the conspecific faced the communicator, while another required the communicator to first attract the attention of a non-attending conspecific. Control conditions tested the probability of orangutans detecting the stimulus on their own and the influence of conspecific presence. Orangutans followed conspecific attention, yet showed no evidence of geometrical conspecific attention following.

7.1 Introduction

Orangutans belong to the great ape clade along with bonobos, chimpanzees, gorillas and humans. While the non-human great apes are often considered as a single group, due to the anatomical and cognitive similarities that distinguish them from monkeys and lesser apes, orangutans are phylogenetically more distantly related to humans, bonobos and chimpanzees than either of those species are to one another (Ruvolo 1997; Wimmer *et al.* 2002). The orangutan clade diverged from the lineage leading to *Pan* and *Homo* 10-12 m.y.a. (Stauffer *et al.* 2001) and represents the best extant model of the last common ancestor of the great apes (Byrne 1995). Orangutans are therefore an ideal species to examine if pleisomorphic (ancestral) or synapomorphic (derived) differences in the following (and directing) of conspecific attention exist within the great ape lineage. Abilities shared by orangutans and the *Pan* species can be assumed to be homologous and represent ancestral states, abilities, or motivations present in the last common ancestor. Conversely, where orangutans can be shown to differ, it may be assumed that these traits are derived and have evolved after the lineage that led to humans and African apes split from the last common ancestor shared with the Pongids.

The majority of research on nonhuman ape communication has involved the African apes, compared to which the gestural communication and socio-cognitive abilities of orangutans are relatively understudied. Compared to the Pan species, orangutans live a mainly semi-solitary lifestyle with loose social bonds. Encounters between males are typically agonistic, while those of females range from affable to mutual avoidance and aggression (Delgado & Van Schaik 2000). In contrast to chimpanzees, both wild and captive orangutans tend to tolerate each other (except for adult males) and engage in few aggressive encounters. While orangutan mothers and offspring typically spend at least 7 years together (until the end of the offspring's juvenile period), where visual and other social communication skills seem essential, adults rarely seek social contact, and adult males spend less than 2% of their time engaging in social activities, such as mating and vocalising (Jantschke 1972, cited by Liebal 2007; Knott 1999).

As sophisticated socio-cognitive skills tend to correlate with the social complexity of primate groups (Whiten & Byrne 1997), some have suggested that the semi-solitary lifestyle of orangutans in densely vegetated forests (Delgado & Van Schaik 2000) may have favoured the importance of tactile and vocal signals over visual signals, and engendered lesser communicative and cognitive skills in *Pongo* than the *Pan* species (Bennett 1998, cited by Liebal *et al.* 2006). While others have argued that small orangutan party sizes owe to feeding competition, and that favourable habitats afford parties similar to those seen in the fission-fusion structure of the *Pan* species (Delgado & van Schaik 2000), the suggestion that visual communication may play a lesser role for orangutans than other great ape species has received implicit empirical support from studies suggesting that orangutans may be less skilful than bonobos and chimpanzees in solving a variety of visual perspective-taking problems, such as the understanding of human experimenters' seeing in the presence of barriers (e.g., Bräuer *et al.* 2005; Okamoto-Barth *et al.* 2007a).

Orangutans, nonetheless, use a number of sophisticated skills in the physical and socio-cognitive domains. Both captive (Lethmate 1982) and wild orangutans (Fox & Bin'Muhammad 2002; van Schaik *et al.* 2003) manufacture and use tools, and possibly, as chimpanzees (Pruetz & Bertolani 2007), deploy javelin tools during hunts (for fish, see Schuster *et al.* 2008). Orangutans pass the 'mark test' for mirror-self recognition (Suarez & Gallup 1981) and show some understanding of what they have (and have not) seen (Call & Carpenter 2001)[45], although, in contrast to chimpanzees and bonobos, seemingly not what they have (and have not) heard (Call

[45] As chimpanzees and 2 year old children, orangutans preferentially look inside the one of two containers that they had not seen baited (Call & Carpenter 2001).

2004). Furthermore, they show some understanding of the intentions underlying others' behaviour, and discriminate between the intentions of experimenters who accidentally or intentionally mark one of two boxes in an object-choice situation (Call & Tomasello 1998).

Orangutans readily follow the gaze and pointing signals of human experimenters to the ceiling (Bräuer *et al.* 2005; Herrmann *et al.* 2007), locations behind themselves (Itakura 1996), and to one of several containers in front of them (Itakura & Tanaka 1998; Byrnit 2004). Moreover, they are sensitive to the attentional state of human experimenters, and alter their signalling modality in accordance with changes in experimenters' attentional focus; They preferentially produce visual gestures when a human faces them (Call & Tomasello 1994; Liebal *et al.* 2004b; Poss *et al.* 2006), and one of two orangutans (the human-reared orangutan, Chantek), in one test showed sensitivity to human eyes, and was more likely to gesture towards food in the presence of an experimenter with open than closed eyes (Call & Tomasello 1994). While orangutans show some understanding of the effect of visual occlusions on humans' visual states (Shillito *et al.* 2005), and have been shown to follow human attention geometrically, around visual barriers (Bräuer *et al.* 2005), one study has failed to find any evidence of this (Okamoto-Barth *et al.* 2007a), leading to the suggestion that orangutans ability within this domain may be less robust as that of the *Pan* species.

The semi-solitary fission-fusion social structure of wild orangutans does not lend itself easily to studies of intra-specific visual signalling, and few studies have been conducted on orangutan conspecific attention following. Observational studies of orangutan sensitivity to the attention of conspecifics concur with experimental findings involving human experimenters. Captive orangutans perform visual-based signals (such as facial expressions and visual gestures) near-exclusively towards attending conspecifics, and use visual gestures more frequently than tactile gestures towards attending recipients (Liebal *et al.* 2006). With respect to gaze patterns, a study of more than 200 gaze episodes during 112 hours of observation recorded only two cases of gaze-following (Kaplan & Rogers 2002), and have (along with observations during sign language teaching: Shapiro & Galdikas 1995), led to the suggestion that orangutans rarely engage in prolonged gazing directly at conspecifics.[46] The typical animal-observer distance in the study was, however, 10m, and given that approximatelyy 65% of the observation time was carried out on free-ranging orangutans in Sabah, Malaysia (which may have made accurate identification of gaze behaviours difficult), the results and conclusions should be treated with some caution. The only available experimental study suggest that orangutans follow the

[46] The same, however, might be said for chimpanzees (personal observation).

attention of conspecifics induced to raise their heads to locations 2m above and immediately behind the subject (Pitman & Shumaker 2009).

The present study aimed to assess the conspecific gaze-following skills of orangutans, for whom little systematic information exists. Secondly, the experiment tested the hypothesis that experimentally naïve orangutans are able and inclined to geometrically follow the gaze of conspecifics (rather than humans), about which no data exists. The experimental and control conditions, and predictions were as detailed in chapters 2 and 5 for chimpanzees and bonobos. It was predicted that there would be a difference between targets animals' looks to the stimulus area during a 30s pre-stimulus phase and a 30s stimulus phase of experimental, but not control trials, and a difference between targets' looks to the stimulus area during the 30s stimulus phases of experimental and control trials. As previous studies have suggested that bonobos and chimpanzees may be more skilled than orangutans at solving a number of visual perspective-taking problems (e.g., Okamoto-Barth *et al.* 2007), it was predicted that orangutans would follow conspecific attention at a lower frequency than chimpanzees and bonobos.

7.2 Methods

7.2.1 Participants

Participants consisted of 7 Bornean orangutans from a group of 8 individuals housed at Twycross Zoo (England). One individual (Tami, 18 months of age) was excluded from the experiment, given near-continual physical contact with its mother. There were three adult females and one adult male ranging from 17-29 years of age (mean age at the start of the experiment = 19 yr., s.d. = 7.16), two juveniles (5 and 7 years) and one infant female (29 months). Six participants were parent-reared and one was hand-reared (Table 7.1). Three adult females had participated in a food receiving experiment (in which their gestures to a human experimenter were recorded) six months prior to testing (Cartmill & Byrne 2007), yet all participants were otherwise experimentally naïve. All of the orangutans, apart from the adult male, were part of a single matriline (led by Kibriah).

Table 7.1: Orangutan participants. The classification of age classes was adopted from Rijksen (1978).

Individual	Sex	Age Class	Age	Date of birth	Rearing history	Mother	Group
Batu	M	Adult	17	25-05-89	Parent	Unknown	Alternate
Kibriah	F	Adult	29	23-01-77	Hand	Jess	1
Maliku	F	Adult	12	10-06-94	Parent	Kibriah	1
Miri	F	Infant	2.5	00-04-04	Parent	Maliku	1
Satu	F	Juvenile	7	31-08-99	Parent	Theodora	2
Theodora	F	Adult	18	05-05-88	Parent	Kibriah	2
Tiga	M	Juvenile	5	22-07-01	Parent	Kibriah	1

Husbandry

The orangutans were housed in two indoor enclosures. During the day they had permanent access (except during cleaning hours) to their core indoor enclosure (approx. 30 m^2) and between the hours of 9 and 16.30 they alternated access to a semi-natural outdoor enclosure of 361 m^2 (Figure 7.1). The outdoor enclosure contained three 12 m tall tree trunks connected by rubber mesh, of which one contained a wooden climbing platform. The enclosure afforded few opportunities for natural foraging, as it contained no natural foliage, and the only growing plant was grass. The animals were fed according to their daily routine with fruits and vegetables, supplemented by primate pellets, vitamins and sweet drinks. In addition, adult the females spent most of the time outdoors picking and eating grass. The keepers provided the apes with

enrichment in the form of plastic bottles, cloth, bags, freshly cut tree branches and cardboard and plastic boxes. The orangutans had auditory access to the public areas, as the outdoor enclosures were separated from these by a 4 m deep moot and approx. 6 m high glass windows. The exhibit received the majority of its visitors between the hours of 10.30-14.30, when several family or school groups observed the animals at any one time. Visitors frequently engaged in calm interactions with the apes. Neither the indoor, nor outdoor enclosures provided a place for the orangutans to be out of view of the public, and all orangutans frequently covered their heads and bodies with the provided cloth.

Figure 7.1: Outdoor orangutan experimental enclosure.

7.2.2 Data collection

The orangutans were tested between the hours of 8.30-16.00 between June and September 2006, and July and August 2007 during a total of approx. 600 hours[47]. While trial durations were brief (60s), the frequent presence of members of the public and the number of conditions that had to be met meant that opportunities to conduct trials were rare. Trials were conducted outside opening hours and at times when few members of the public present, between the hours of 8.30-10.30 and 14.30-16.00.

[47] Orangutans and bonobos were tested during a total of 1,523 observation hours, of which approx. 40% (609 hours) of the time was spent with the orangutans and 60% (914 hours) with the bonobos.

7.2.3 Design, Materials and Procedure

The general methods were as detailed in chapter 2 (Attention following in chimpanzees), and consisted of the same two experimental conditions (*'Target faces communicator'* and *'Target faces away from communicator'*) and five control conditions *('No Stimulus-Target faces towards communicator', 'No Stimulus-Target faces away from communicator', 'Target Alone', 'Target and Ignorant Communicator', 'Communicator Alone'*, Figures 7.3-7.9). The experimenter projected a visual stimulus into the participants' enclosure; a moving light pattern within an area of approx. 0.5m^2, produced by a commercial green 3b laser pointer (OnPoint Extreme Fusion: 532 nm; power output: 125 mW, point diameter at 4 m distance in ambient outside light: approx. 2 cm). The stimulus was identical to the one used in the experiment involving bonobos (Chapters 5 and 6). Ninety-five percent of trials were conducted outside. Five percent of trials (5 of 98) were conducted inside and the stimulus displayed in three of the trials and viewed by subjects in two trials (3% and 2% of the total number of trials, respectively, see Appendix 2 for pictures of inside enclosures). The stimulus was projected from the public areas onto 28 different locations in the experimental enclosure (Figure 7.9).

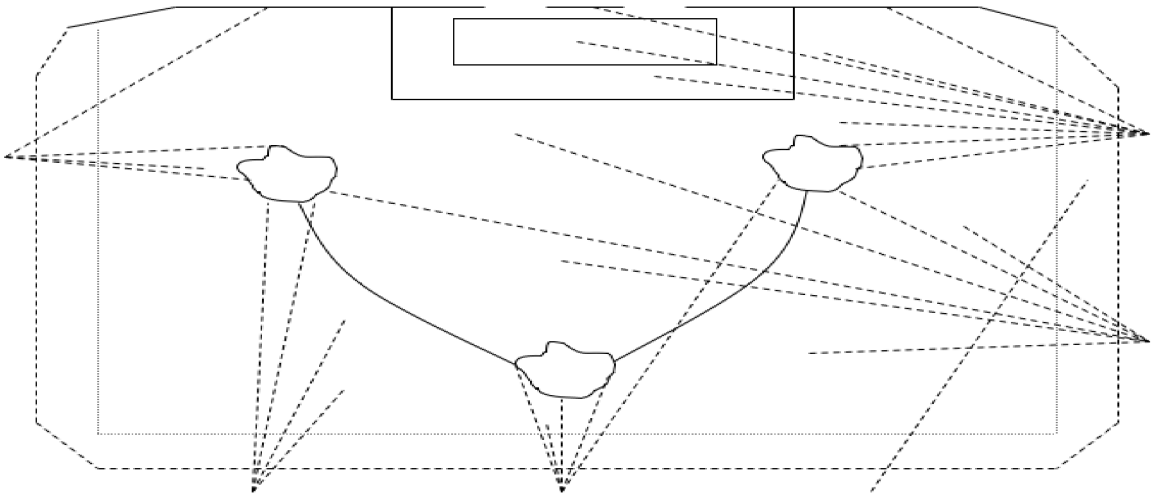


Figure 7.2: The use of the outside experimental enclosure. Dotted lines indicate windows, where the ground slants into a moat (see also Figure 7.1), and stimulus projection points at 28 different locations, projected from the public areas. Illustrations depict three horizontal wooden logs connected by rubber mesh

Figure 7.3: Experimental condition: '*Target faces communicator*'. (Still of stimulus [i.e., only a dot, not a pattern is visible in the still] is encircled).

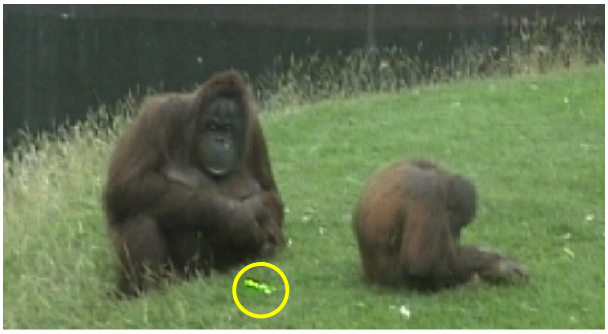


Figure 7.4: Experimental condition: '*Target faces away from communicator*'.

Figure 7.5: Control condition: '*No Stimulus – Target faces communicator*'. The stimulus is aimed on the grass behind the target.

Figure 7.6: Control condition: '*No Stimulus – Target faces away from communicator*'. The stimulus is aimed on the grass in front of the communicator.

Figure 7.7: Control condition: *'Target Alone'*.

Figure 7.8: Control condition: '*Target and Ignorant Communicator*'.

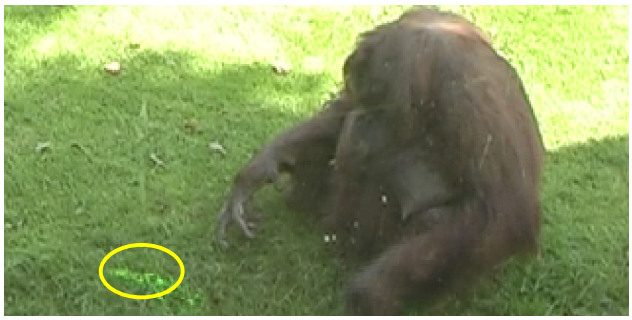


Figure 7.9: Control condition: *'Communicator Alone'*.

Trials requiring targets to turn versus locomote to detect the stimulus

Sixty-one percent (60 of 98) of trials required targets to only turn around to see the stimulus, while 39% (38 of 98) that they first locomote around a visual barrier (Table 7.2). The two trial types were not designed conditions, but due to the nature of the experimental set-up.

Table 7.2: Trials requiring targets to 'locomote' and 'turn' to look to the stimulus.

Condition	Percent		N	
	Turn	Locomote	Turn	Locomote
Experimental	57	43	16	12
No Stimulus	64	36	18	10
Target Alone	80	20	12	3
Target & Ignorant Communicator	52	48	14	13
Total	61	39	60	38

Trial sequences

The conditions were presented sequentially in an order determined as detailed in section 2.2.2.4). Some targets with dependent offspring were never alone and could not be tested individually; for these individuals, *'Target Alone'* trials were substituted by *'Target and Ignorant Communicator'* trials. All individuals received two trial sequences (Table 7.3)

Table 7.3: Trial sequences and order of presentation of trials; EXP = '*Experimental*', NOS = '*No Stimulus*', TAR = '*Target Alone*', TAR+ = '*Target and Ignorant Communicator*', COM = '*Communicator Alone'*, T = Target faces *towards* communicator, A = Target faces *away* from communicator. Coloured text indicates trials involving a stimulus.

Participant	Trial Sequence	1	2	3	4	5	6	7	8
Batu	1	TAR+	COM	EXP T	NOS A	EXP A	NOS T	TAR	TAR
	2	NOS A	TAR+	TAR	COM	EXP A	TAR	EXP T	NOS T
Kibriah	1	COM	NOS A	TAR+	NOS T	EXP T	TAR+	EXP A	TAR+
	2	TAR	EXP T	EXP A	TAR+	TAR	NOS A	COM	NOS T
Maliku	1	TAR+	COM	EXP A	NOS T	EXP T	NOS A	TAR+	TAR
	2	NOS T	TAR	NOS A	EXP A	TAR+	TAR+	EXP T	COM
Miri	1	TAR+	TAR+	NOS T	COM	TAR+	EXP A	NOS A	EXP T
	2	TAR+	EXP A	TAR+	NOS A	COM	EXP T	TAR+	NOS T
Satu	1	NOS A	TAR	EXP T	TAR	COM	TAR+	NOS T	EXP A
	2	TAR	EXP A	TAR	NOS T	TAR+	COM	EXP T	NOS A
Theodora	1	COM	TAR+	NOS T	TAR+	NOS A	EXP T	EXP A	TAR
	2	COM	NOS A	EXP T	TAR	NOS T	TAR	TAR+	EXP A
Tiga	1	TAR+	NOS T	COM	EXP T	NOS A	EXP A	TAR+	TAR+
	2	TAR+	TAR+	COM	EXP T	TAR+	EXP A	NOS T	NOS A

7.2.4 Scoring and reliability

I coded whether the stimulus area fell within targets' 'open' field of vision during the pre-stimulus and stimulus phases, and a second coder coded 40% of the trials for reliability purposes (100 % [N = 28] of experimental trials and 17% [N = 70] of a random selection of control trials). Inter-observer reliability was very good (pre-stimulus phase: Cohen's kappa = 94.56, n = 39; Stimulus phase: Cohen's kappa = 0.88, n = 39).

7.2.5 Statistics

The general rationale for the choice of statistical analyses is detailed in Chapter 2, section 2.2.2.6. Repeated measures binomial logistic regressions (GLMM) were used for analyses of targets' looks to the stimulus area during the pre-stimulus and stimulus phases of experimental and control conditions, respectively, and to compare looks to the stimulus area during the stimulus phases of experimental and control conditions. Moreover, individuals' performance of the pre-stimulus and stimulus phases of the first trial received in individual conditions was analysed by means of non-parametric McNemar tests for repeated measures and nominal data. Null-hypotheses were rejected at an alpha level of 5%, and all tests were two-tailed.

7.3 Results

Orangutans followed the attention of conspecifics to the stimulus in 42.86% (6 of 14) of trials when the conspecific viewed the stimulus, 71.42% (5 of 7) and 14.29% (1 of 7), respectively, in trials where they faced *towards* and *away* from the communicator at the start of stimulus projection (percentage is based on the first trial that communicators received in the two *experimental* conditions). Communicators produced a visible behaviour while within targets' 'open' or 'peripheral' field of vision (approached, extended hand towards or touched the stimulus, alternated gaze between the stimulus and target, repositioned body while looking at stimulus, or arrested current behaviour) in 28.57% (4 of 14) of *experimental* trials (percentage based on the first trial received in the two experimental conditions). Although based on very few observations, orangutans followed communicator attention in 100% (3 of 3) *experimental* trials where conditions were comparable to those, under which the intra-specific attention following of five other primate species have been tested (Tomasello *et al.* 1998), and only trials (i) where the communicator produced a visible behaviour while being within the targets' 'open'

or 'peripheral' field of vision, (ii) targets faced *towards* the communicator at the start of trials, and (iii) were required to only 'turn' around to look to the stimulus.

Comparisons within conditions (of pre-stimulus and stimulus phases - 'Pre versus post' control):

Orangutan targets were more likely to look to the stimulus area during the stimulus than pre-stimulus phase of *experimental* trials (GLMM: Estimate = 2.28, SE = 0.87, z = 2.62, p = 0.01). When the experimental conditions where the target faced *towards* and *away* from the communicator at the start of the stimulus phase were analysed separately, targets were more likely to look to the stimulus area during the stimulus phase of trials where they faced *towards* (All trials received, GLMM: Est. = 2.57, SE = 1.17, z = 2.20, p = 0.028; Analysis of first trial received, McNemar test: χ^2 = 5.79, N = 7, p = 0.016), but not *away* from the communicator at the start of trials (All trial received, GLMM: Est. = 2.63, SE = 1.67, z = 1.57, p = 0.116; Analysis of first trial, McNemar test: χ^2 = 0.07, N = 7, p = 0.789). There were no significant differences in the likelihood of targets looking to the stimulus area during the pre-stimulus and stimulus phases of the control trials (see Table 7.4a and Figure 7.10).

Considering the duration of looks, targets overall oriented significantly longer (i.e., the stimulus fell within the targets' 'open' field of vision) towards that stimulus area during the stimulus phase (mean = 9.33s, s.d. = 9.12) than pre-stimulus phase of experimental trials (mean = 1.42s, s.d. = 3.48, t(12) = -2.58, $p < 0.05$, repeated measures t-test conducted on trials where targets looked to the stimulus area during either the pre-stimulus or stimulus phase).

Comparisons across conditions (of looks to the stimulus area during stimulus phases):

There was no significant difference between targets looking to the stimulus when displayed outside the view of a '*Target Alone*' and a '*Target and Ignorant Communicator*' (comparison of stimulus phases of all trials in the two conditions: N = 42, p = 1). The '*Target Alone*' and '*Target and Ignorant Communicator*' conditions were therefore collapsed. Targets were more likely to look to the stimulus area during the stimulus phase of experimental than control conditions (All trials received: GLMM with 'look/no-look/, '*Experimental*', '*No Stimulus*' and '*Target Alone*'/'*Target and Ignorant Communicator*' conditions entered as factors and participant as a random factor: '*Experimental*' vs. '*No Stimulus*' (GLMM: Est. = -2.86, SE = 1.09, z = 2.62, p = 0.000; '*Experimental*' vs. '*Target Alone*'/'*Target and Ignorant Communicator*': Est. = -1.82, SE = 0.65, z = 2.78, p = 0.005, Figure 7.10, Table 7.4b).

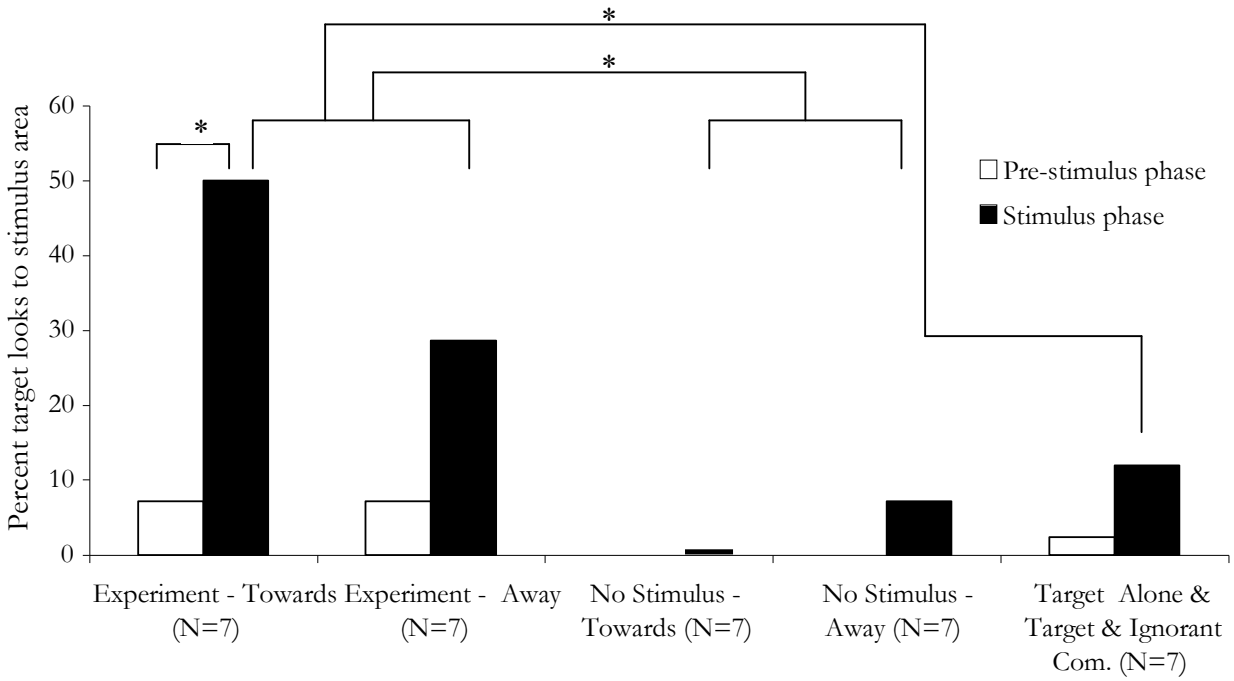


Figure 7.10: Target looks to the stimulus location. Percent target looks to the stimulus area during the pre-stimulus and stimulus phases of experimental and control conditions (percentages are based on the average response to the trials that individual subjects received). Asterisks indicate significant differences between target looks to the stimulus location during stimulus and stimulus phase of '*experimental-towards*' trials, and during the stimulus phases of *experimental* and control trials.

Trials requiring targets to turn around to look to the stimulus

Comparisons within conditions (of pre-stimulus and stimulus phases - '*Pre versus post*' control):

Considering the subset of trials that required targets to only turn around, so as to look to the stimulus (61% of all trials, 60 of 98), orangutan targets were significantly more likely to look to the stimulus area during the stimulus phase than pre-stimulus phase of *experimental* trials (GLMM: Estimate = 2.77, SE = 0.94, z = 2.97, $p = 0.003$). This result remained when trials, in which target animals faced *towards* (GLMM: Est. = 3.33, SE = 1.33, z = 2.51, $p = 0.012$; Analysis of first trial, McNemar test: $\chi^2 = 10.08$, n = 6, $p = 0.002$), but not *away* from the communicator at the start of the stimulus projection were considered separately, although the latter approached significance when all received trials were analysed (GLMM: Est. = 2.69, SE = 1.52, z = 1.77, $p = 0.077$; Analysis of first trial, McNemar test: $\chi^2 = 0.90$, n = 5, $p = 0.343$). There were no significant differences between targets looking to the stimulus area during the pre-stimulus and stimulus phases of controls trials (see Table 7.4b).

Comparisons across conditions (of looks to the stimulus area during stimulus phases):

Targets were more likely to look to the stimulus area during the stimulus phase of the *experimental* than control conditions (All trials received: *Experimental*' vs. '*No Stimulus*': GLMM: Est. = -3.63, SE = 1.16, z = 3.12, $p = 0.002$; '*Experimental*' vs. '*Target Alone*'/'*Target and Ignorant Communicator*': Est. = -2.83, SE = 0.82, z = 3.46, $p = 0.001$, Figure 7.11).

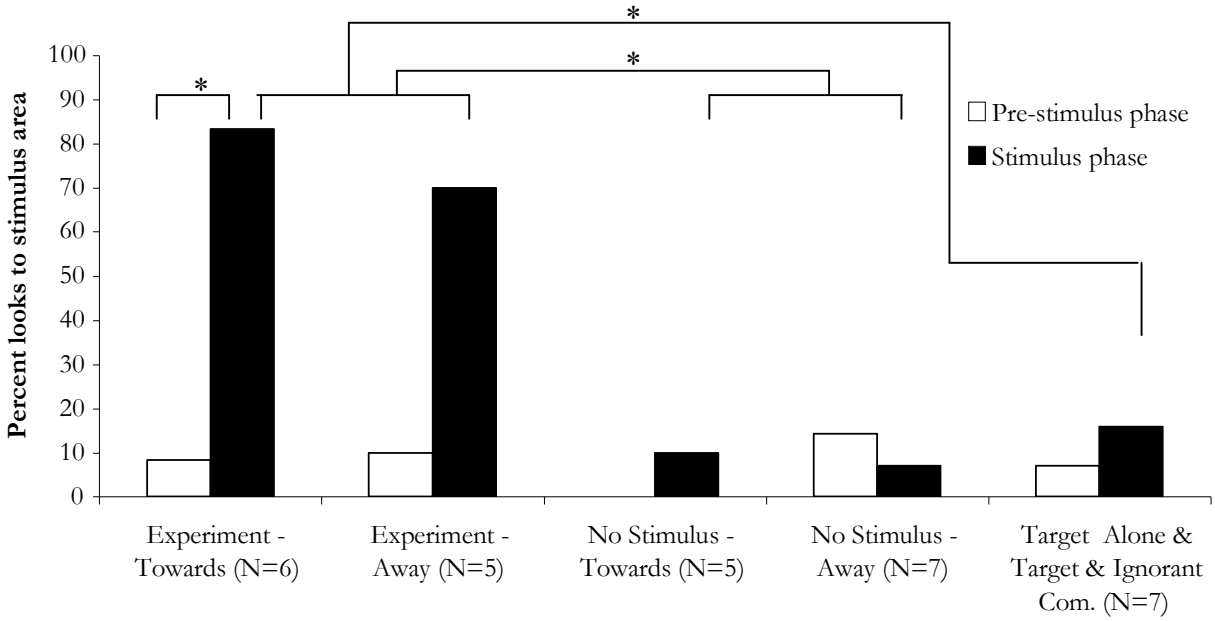


Figure 7.11: Turn trials. Percent target looks to the stimulus area during the pre-stimulus and stimulus phases (based on the average response to all 'turn' trials that individuals received; As some subjects did not receive 'turn' trials in all conditions, N vary). Asterisks indicate significant

differences across conditions.

Trials requiring targets to locomote around a barrier to look to the stimulus

Considering only the subset of trials that required targets to first locomote around a visual barrier to look to the stimulus (39% of all trials, 38 of 98), targets looked to the stimulus in 0% (0 of 12) of *experimental* trials (and in one control trial, '*Target and Ignorant Communicator*'). There were, thus, no significant differences between targets looking to the stimulus area during the pre-stimulus and stimulus phases of neither experimental nor control conditions, nor during the stimulus phases of the different conditions (Table 7.4c).

Table 7.4: Results summary. Statistics for all trials (Table a), and for the data-subsets where targets were required to either only 'turn' (Table b), or to 'locomote' around a barrier to look to the stimulus (Table c). The hypotheses predicted a difference between target looks to the stimulus locations in comparisons 1-3 and 7-8, and none in comparisons 4-6. Significant (and one near-significant) differences are highlighted in grey.

a) All Trial type(s) compared	Intervals compared	GLMM				McNemar Test (first trial received)	
		Estimate	**SE**	**Z**	***P***	χ^2	***P***
1 Experimental (all trials)	Pre- & Stimulus	2.28	0.87	2.62	0.001		
2 Exp. - Target faces towards com.	Pre- & Stimulus	2.57	1.17	2.20	0.028	5.79	0.016
3 Exp. - Target faces away from com.	Pre- & Stimulus	2.63	1.67	1.57	0.116	0.07	0.789
4 No Stimulus - Target faces towards com.	Pre- & Stimulus	0.00	134600	0.00	1.000	0.03	0.789
5 No Stimulus - Target faces away from com.	Pre- & Stimulus	18.00	7812	0.00	0.998	0.07	0.789
6 Target Alone / Target & Ignorant com.	Pre- & Stimulus	1.46	1.14	1.28	0.200	2.77	0.092
7 Exp. & No Stimulus	Stimulus	-2.86	1.09	2.62	0.009		
8 Exp. & Target Alone/Target & Ign. com.	Stimulus	-1.82	0.65	2.78	0.005		

b) 'Turn' trials Trial type(s) compared	Intervals compared	GLMM				McNemar Test (first trial received)	
		Estimate	**SE**	**Z**	***P***	χ^2	***P***
1 Experimental (all trials)	Pre- & Stimulus	2.77	0.94	2.97	0.003		
2 Exp. - Target faces towards com.	Pre- & Stimulus	3.33	1.33	2.51	0.012	10.08	0.002
3 Exp. - Target faces away from com.	Pre- & Stimulus	2.69	1.52	1.77	0.077	0.90	0.343
4 No Stimulus - Target faces towards com.	Pre- & Stimulus	0.00	190400	0.00	1.000	0.10	0.752
5 No Stimulus - Target faces away from com.	Pre- & Stimulus	18.26	8813	0.00	0.998	0.07	0.789
6 Target Alone / Target & Ignorant com.	Pre- & Stimulus	0.18	1.19	0.99	0.321	2.29	0.131
7 Exp. & No Stimulus	Stimulus	-3.63	1.16	3.12	0.002		
8 Exp. & Target Alone/Target & Ign. com.	Stimulus	2.83	0.82	3.46	0.001		

c) 'Locomote' trials Trial type(s) compared	Intervals compared	GLMM				McNemar Test (first trial received)	
		Estimate	**SE**	**Z**	***P***	χ^2	***P***
1 Experimental (all trials)	Pre- & Stimulus	0.00	145400	0.00	1.000		
2 Exp. - Target faces towards com.	Pre- & Stimulus	0.00	136600	0.00	1.000	0.13	0.724
3 Exp. - Target faces away from com.	Pre- & Stimulus	0.00	190400	0.00	1.000	0.10	0.752
4 No Stimulus - Target faces towards com.	Pre- & Stimulus	0.00	190400	0.00	1.000	0.10	0.752
5 No Stimulus - Target faces away from com.	Pre- & Stimulus	0.00	176400	0.00	1.000	0.17	0.683
6 Target Alone / Target & Ignorant com.	Pre- & Stimulus	17.86	7308	0.00	0.998	0.45	0.230
7 Exp. & No Stimulus	Stimulus	0.00	20640	0.00	1.000		
8 Exp. & Target Alone/Target & Ign. com.	Stimulus	18.86	13910	0.00	0.999		

7.4 Discussion

As predicted, orangutans readily followed conspecific attention in face-to-face situations. Although the stimulus shown to the communicator was removed immediately before it fell within the peripheral view of the attention following individual, individuals oriented longer towards the stimulus area during the stimulus than pre-stimulus phase of experimental trials, suggesting an expectation of a point of interest. In contrast, orangutans were no more likely than chance to look to the stimulus when they faced *away* from the individual, who viewed the stimulus, and was therefore required to, somehow, first attract the other's attention.

Orangutans followed the gaze of conspecifics in 71% of trials when they faced the conspecific (compared to 60% and 45% for chimpanzees and bonobos, respectively) disconfirming the hypothesis that the orangutans would follow conspecific attention at a lower frequency than the populations of chimpanzees and bonobos tested (see Chapter 9 for a direct test of potential species differences). This is consistent with a previous finding that conspecific orangutan gaze following does not differ from that of other great apes induced to raise their heads to locations 2m above and immediately behind the subject (Pitman & Shumaker 2009).

Where conditions where comparable to those, under which the intra-specific gaze following of e.g., mangabeys and macaques have been tested (Tomasello *et al.* 1998), orangutans followed conspecific attention in 100% trials (compared to 78% and 73% for chimpanzees and bonobos, detailed in Chapters 2 and 5), yet the number of trials that matched this criterion was too small, to allow any species comparisons to be drawn. The rate of following the attention of conspecifics in face-to-face contexts in the present experiment (71% for the first received trial and 50% when all [two] received trials were considered) considerably exceeds the 33% (Bräuer *et al.* 2005) and 50% (Pitman & Shumaker 2009) found when orangutans have faced a human experimenter looking to the ceiling. It also exceeds the gaze following rate of 35% found when conspecifics were induced to raise their heads to locations 2m above and immediately behind the subject (Pitman & Shumaker 2009).

One cause of the seeming difference of results across these and the current study may lie in the number of trials that the apes received. The present results relied on fewer trials (percentages were based on one and two trials, respectively), than previous experiments (Bräuer *et al.* 2005; Pitman & Shumaker 2009), which involved six trials presented to each subject in relative quick succession. The subjects in Bräuer and colleagues' and Pitman & Shumaker's experiments may to some extent have habituated to the experimenter's looks to the ceiling

(given the absence of an interesting target) and to a conspecific's repeated looks to an experimenter holding up a wooden block, thereby producing an overall lower rate of gaze following than in the present experiment. The rate of attention following in the present experiment may thus be more representative for the species, as it was not part of an on-going (food-delivery-related) interaction (Bräuer *et al.* 2005), and not influenced by potential habituation effects (Bräuer *et al.* 2005; Pitman & Shumaker 2009). It should, nonetheless, be emphasized that the orangutan communicators in the present experiment produced behaviours indicative of their focus of attention, other than only head and gaze orientation.

While previous research has demonstrated that orangutans with considerable experimental experience follow the gaze or pointing signals of human experimenters (Itakura 1996; Itakura & Tanaka 1998; Byrnit 2004; Bräuer *et al.* 2005; Herrmann *et al.* 2007), the present experiment presents consistent and systematic observations of conspecific gaze following by orangutans. The results support the results of an observational study recording two instances of gaze following during 112 hours of observation (Kaplan & Rogers 2002), and the recent finding that orangutans follow the attention of conspecifics induced to raise their heads towards an item held by a human 2m above and immediately behind the subject (Pitman & Shumaker 2009). Moreover, the results show that co-orientation of attention consistently occurs in the interactions between experimentally naive animals, to points that require a only small reorientation on the part of the communicator and where no interesting events (such as human presence) typically occur.

Orangutans showed no evidence of being able/inclined to follow the attention of conspecifics geometrically. While this result concurs with research suggesting that orangutans show limited understanding of the referential nature of *human* gaze in the presence of transparent and opaque barriers (Okamoto-Barth *et al.* 2007a), it is contradicted by another finding that orangutans do follow human gaze around opaque barriers (Bräuer *et al.* 2005). The findings by Bräuer and colleagues are, however, not fully comparable to the present results, as the gaze following in that experiment occurred as part of an ongoing communicative interaction between the human and orangutan, involving the cessation of provision of a significant reinforcer, food. In the experiment, the human repeatedly fed the subject pieces of food, until, while holding a piece of food in hand, she arrested behaviour, and for 1 minute looked to a location behind a barrier, outside the subject's view, while alternating head and gaze between the subject and target. The withholding of food is likely to have strengthened the subjects' response, and the experimenter's gaze alternation added a communicative signal that prevents

conclusions being drawn, as to whether the subject responded to the experimenter's attention alone, or the intentionally communicative signal. While the results suggest that orangutans with considerable experimental experience follow human attention geometrically in food provisioning contexts (Bräuer *et al.* 2005), their failure to do so outside ongoing communicative interactions involving immediate food rewards (i.e., in the present experiment and the study by Okamoto-Barth and colleagues), suggests that motivational factors may be at play. It raises the question, as to whether orangutans' seemingly poorer performance on geometrical attention following trials, compared to bonobos and chimpanzees (in the study by Okamoto-Barth and colleagues, and as suggested by the performance of the orangutans and bonobos tested in the current experiment), owes to motivational rather than cognitive factors, and lie in the comparatively less motile behaviour of the species.

The results suggest that although the orangutans re-oriented in response to conspecific attention to the stimulus, this may have occurred purely on the basis of adventitious cues, without active attraction of conspecific attention, and production of intentionally communicative cues on the part of the communicator. The next chapter will further explore whether, and if so, which, particular behaviours produced by communicators consistently led to conspecific attention re-orientation, and potential intentionality underlying such behaviours.

CHAPTER 8: An experimental study of orangutan manipulation of conspecific attention

Summary

The behaviour of 7 Bornean orangutans who were presented with a novel visual stimulus while either alone or in the presence of an attentive or non-attentive conspecific (see Chapter 7) was recorded. Contrary to prediction, there was no difference in the production of gaze behaviours, auditory, locomotory and visual stimulus directional behaviours across the three conditions, and none of the behaviours predicted whether conspecifics looked to the stimulus. There was no species-wide evidence for active attention calling followed by directional signalling, although two orangutans followed sequential auditory-stimulus-directional behaviour by gaze shifts between the stimulus and an initially non-attentive conspecific, who then co-oriented to animal's attention to the stimulus area. Moreover, in a few cases orangutans may have used gaze communicatively.

8.1 Introduction

The largely solitary and individually based fission-fusion structure of wild orangutans does not lend itself readily to examinations of intra-specific visual signalling, and many studies have thus focused on vocal communication (e.g., McKinnon 1974; Galdikas & Insley 1988; Mitani 1985). While studies of wild and reintroduced orangutans suggest that they use a range of vocal signals and often incorporate auditory displays (such as throwing, slapping and shaking branches), an extensive observational study of captive orangutans found a complete absence of auditory signals (Liebal *et al.* 2006). In contrast, orangutans frequently produce auditory signals (object or cage bang, clap or 'kiss squeak', 'raspberry') in experimental studies, to solicit human attention (Poss *et al.* 2006; Cartmill & Byrne 2007). Observational studies of the gestural communication of wild (MacKinnon 1974; Kaplan & Rogers 2002), reintroduced (Rijksen 1978; Bard 1992) and captive orangutans (Liebal *et al.* 2006; Liebal 2007 Genty *et al.* 2009) indicates a variable and flexibly used gestural repertoire, with a higher proportion of tactile signals than

those of chimpanzees and bonobos (Liebal *et al.* 2006; Genty & Byrne 2009). While orangutans frequently repeat their gestures, combining them into sequences, such sequences comprise mainly of repetitions of the same signal rather than elaborations or functionally different signals (Liebal *et al.* 2006; Genty & Byrne 2009).

Attention and communicative gestures

Both observational (Liebal *et al.* 2006; Genty *et al.* 2009) and experimental studies (Call & Tomasello 1994; Poss *et al.* 2006) show that orangutans (as chimpanzees: Hostetter *et al.* 2001; Leavens *et al.* 2004) deploy appropriate communicative signals to gain others' attention, and preferentially use visual signals (facial expressions and visual gestures) when the receiver attends to them, and auditory and tactile signals when not. Overall, research suggests that orangutans discriminate between the different states of visual attention in others and have some understanding of the effectiveness of their signals.

While orangutans may use signals to intentionally attract the attention of human experimenters, neither intra-specific observational studies (Liebal *et al.* 2007; Genty & Byrne 2009), nor inter-specific experimental study (Liebal *et al.* 2004b) have found evidence that orangutans use attention-getting behaviours to capture the attention of non-attending individuals (i.e., make the recipient move to face them) before producing a more specific visual signal, such as begging. Interestingly, when presented with un-reachable food and an experimenter oriented either towards or away from the subject, chimpanzees and bonobos tend to change their own relative orientation and move to gesture in front of the experimenter, while orangutans continue to gesture predominantly towards the location of the food (Liebal *et al.* 2004a). While this suggests that apes find it less difficult to change their own relative orientation than manipulate human attentional orientation (Gómez 2005), it indicates that the sensitivity to human orientation, when deploying visual gestures, either may be higher in the *Pan* species than *Pongo* (as suggested by e.g., Liebal *et al.* 2004b), or as seems more likely in the light of the *Pongids* overall less 'active' way of life, that orangutans may simply be overall less motivated to locomote. That is, rather than the different performance of the *Pongo* and *Pan* species on these tasks reflecting species differences in cognition, it seems reasonable (and parsimonious) to conclude that the observed differences rely on motivational factors.

Orangutans (like chimpanzees: Leavens *et al.* 2005) also modify their communicative strategies according to the responses and apparent comprehension by their human audience (Cartmill & Byrne 2007). When in the context of food begging, presented with experimenters

who appear to understand the orangutans' request for food (i.e., deliver food), partially-understand (deliver half of the food), or misunderstand their requests (deliver alternative, less desirable food), orangutans select different tactics for repairing the apparently failed communication. When partially understood, they repeat the same or similar signals more energetically, while when misunderstood, they switch to a tactic of using a wider range of different gestures, and avoid those initially used. Such accommodation of communicative tactics suggests that orangutans, not only view others as agents capable of having intentions and perceptions, but also that they communicate intentionally about distal objects.

Inter-specific pointing

More than 30 years of field studies have provided no evidence that orangutans produce and use pointing gestures in a referential way during interactions with conspecifics. Many captive orangutans with experience of physical barriers and being placed in a position unable to acquire food or objects, however, (like other apes) develop tactics to request unreachable food from humans (e.g., Gómez & Teixidor 1992, cited by Gomez 1996; Call & Tomasello 1994). Moreover, anecdotal descriptions suggest that human-raised orangutans may point distally to things other than food, including other humans (Furness 1916)[48], objects they desire, and places they wish to travel (Miles 1990). Orangutans who have received training in pointing also appear capable of more complex forms of referential signalling, as both mother- as human-reared orangutans will guide a human experimenter to the location of a hidden tool needed to access food for the animal (Gómez & Teixidor 1992; Call & Tomasello 1994; Zimmermann *et al.* 2009). While this behaviour suggests that the animals may be motivated by an either informative motive or a complex imperative request that the human recover and use to tool to retrieve food (Gómez 2004; Zimmermann *et al.* 2009), the finding that the animals frequently pointed to the tool when the human experimenter knew the location of the tool (i.e., when informational pointing was not necessary), suggests that their behaviour did not reflect the mind-reading skills required for informative pointing (Zimmermann *et al.* 2009).

Declarative pointing has only been anecdotally reported for the human-raised, language-trained orangutan, Chantek, for whom the acquisition of pointing seemed to follow a typical human sequence (Miles 1990). The superior performance of Chantek over mother-raised

[48] "When asked "where is papa " she [an orangutan] would at once point to me or pat me on the shoulder" (Furness 1916, p. 284).

orangutans in a number of experiments (e.g., representing the mental state of another by distinguishing intentional from accidental actions: Call & Tomasello 1998; production and comprehension of pointing: Call & Tomasello 1994; preferentially requesting food from experimenters with open versus closed eyes: Call & Tomasello 1994) and of other 'enculturated' orangutans (Itakura & Tanaka 1998) has, however, lent support to the suggestion that individuals, raised with extensive human contact in early ontogeny, display more complex forms of cognition (Call & Tomasello 1996). Although the underlying mechanisms, by which human rearing influences developing apes remain obscure, it is plausible that the triadic interactions characteristic of human communication (involving the ape, human and an object of joint attention) facilitate the development of perspective taking, understanding of intentionality and learning about communicative intentions (Tomasello 1995).

Intra-specific pointing

While there is no evidence of orangutans pointing for one another in their natural habitats, individuals who have been previously trained to point by keepers and experimenters can generalize the behaviour to point imperatively amongst themselves. In a study, where orangutans were placed in neighbouring cages and had to request out-of-reach tokens from conspecifics, to subsequently exchange them with experimenters for food, individuals used hand begging and imperative manual pointing (fingers extended through the mesh separating the cages) in direction of the tokens, which appeared to be understood and rewarded as requests by conspecifics (Pele *et al.* 2009). It does, however, remain equivocal whether the behaviour involved understanding of the socio-cognitive causality underlying the gestures' efficacy upon the behaviour of others, or were simply conditioned responses with little understanding of the reason for their effectiveness (i.e., that the gesture functioned to *indicate* a want: Gómez 2004). While the finding is intriguing and represents the only reported instance of pointing amongst orangutans, the token transfer experiment involved the same orangutans as tested by Zimmermann and colleagues (Zimmermann *et al.* 2009), that all had extensive experience with physical barriers and being placed in a position unable to acquire food or objects by themselves. Thus, all individuals were used to point to objects to indicate a choice, or request unreachable, food from human experimenters, and the behaviour may therefore have required only a generalisation to a different (species of) recipient. Moreover, the indication (in another experiment) that additional experience with the particular experimental setup enabled a mother-raised orangutan to eventually respond appropriately to cues also used by an 'enculturated' orangutan (e.g., open vs. closed eyes: Call & Tomasello 1994), suggests that rather than

engendering more complex cognition, 'enculturation' and extensive human contact, including training and experience with the experimental setups, may simply increase the opportunity for learning about the peculiarities of human interaction and communication channels. If so, it would lend support to the notion that intra-specific pointing in experimentally experienced orangutans does not represent a qualitative departure from other forms of imperative communication amongst orangutans.

Aim

Surprisingly few experiments have involved orangutans without extensive human and laboratory experience, and only two previous experimental studies of orangutan communication (Pele *et al.* 2009; Pitman & Shumaker 2009) have involved conspecifics rather than only humans. The results of the previous chapter suggest that, although orangutans re-orient in response to conspecific attention to a novel stimulus, this may have occurred purely on the basis of adventitious cues emitted by individuals viewing the stimulus, without active attraction and redirection of non-attending conspecifics. This chapter aims to explore whether behaviours produced by orangutans viewing the novel stimulus consistently led to conspecific attention re-orientation, and whether individuals intentionally redirected conspecifics' attention. To test if communicators actively called the attention of non-attentive conspecifics, and led them to look to a stimulus that only they observed, the method and rationale presented in Chapter 3 (Attention Following in Chimpanzees) was used to record, whether communicators produced different behaviours or combinations thereof when in the presence of the stimulus but absence of a conspecific, and in the presence of the stimulus and an either attentive or non-attentive conspecific. As in Chapter 3, it was predicted that communicators would behave differently as a function of conspecific's presence and visual attention.

By virtue of orangutans' willingness to cooperate with conspecifics (Pele *et al.* 2009) and to obtain rewards for conspecifics as themselves (Chalmeau *et al.* 1997), one might predict cooperative abilities similar to those of bonobos. Given differences in social structure and performance in social cognition experiments, orangutans were, however, predicted be less likely than chimpanzees and bonobos to intentionally direct conspecifics to the novel stimulus and engage in referential signalling.

8.2 Methods

8.2.1 Design and procedure

The analyses were based on the experiment described in Chapter 7, involving 7 orangutans, and followed the rationale described in Chapter 3. The key comparisons involved the *experimental* and '*Communicator Alone*' conditions, designed to test if communicators took conspecific presence and attentional state into account when responding to the stimulus. The conditions were presented in an order determined by the Latin Square technique (see to Figure 7.3), in which 86% (N = 7) of participants received a '*Communicator Alone*' control trial before the first *experimental* trial.

8.2.2 Coding of communicator behaviour

The communicator behaviours coded were as detailed in Chapter 3 and 6 (in studies of chimpanzees and bonobos), and comprised of (1) auditory, (2) visual non-stimulus directional, (3) visual stimulus directional, (4) locomotory stimulus directional (approach), and (5) conspecific directional gaze behaviours (Table 8.1, see also section 3.2.2 for further definitions of individual behavioural categories).

Table 8.1: Behavioural categories coded.

Behaviours Class	**Behaviour**
(1) Auditory	Voalise, stamp, knock, clap, move object
(2) Visual non-stimulus directional	Arrest beahviour, swagger, shake extreity, shake object, bob head, hea
(3) Visual stimulus directional	Touch, lean, exend extremity, move head forward, 'hunch'
(4) Locomotory stimulus directional	Approach
(5) Conspecific directional	Gaze 1: Signaller looks to conspecific within 2s of looking to the stim Gaze 2: Signaller looks to a conspecific within 2s of looking to the stimulus, followed by a look to the stimulus within 2s of looking awa the conspecific (gaze behaviour: stimulus-target-stimulus). Gaze chan scored by head movement and only trials scored unequivocallly are included.

8.2.3 Scoring and reliability

A second coder coded a random selection of 17% (7 of 42) of *experimental* and '*Communicator Alone*' trials to assess inter-observer reliability in terms of (1) auditory, (2) visual stimulus directional, and (3) locomotory stimulus directional behaviours. Inter-observer reliability with respect to auditory and visual stimulus directional cues was perfect (Cohen's kappa = 1, n = 7), while it was 'good' with respect to auditory cues (Cohen's kappa = 0.70, n = 7).

8.2.4 Statistics

In contrast to chimpanzees and bonobos tested, all orangutans received two full sequences of trials. To deal with the issue of potential pseudo-replication caused by each participant receiving two '*Experimental-Towards*', '*Experimental-Away*' and '*Communicator Alone*' trials, the distribution of communicators' behaviours across the thee conditions, and of targets' look to the stimulus area when communicators produced particular behaviours, were analysed by means of repeated measures binomial logistic regressions (fitted by the Laplace approximation). Gaze behaviours were analysed by means of binomial tests. Null-hypotheses were rejected at an alpha level of 5%.

8.3 Results

8.3.1 Communicator behaviour

There was no statistical significance in the production of any of the recorded behaviours across the three conditions (Table 8.2, Figure 8.1). Locomotory stimulus directional behaviours, however, approached significance for the '*Communicator Alone*' condition, and visual *non*-stimulus directional behaviours approached significance for when the communicator viewed the stimulus in the presence of a *non*-attentive conspecific ('*Experimental-Away*'). Likewise, there was a trend for communicators to produce stimulus directional behaviours more frequently when viewing the stimulus in the presence of a *non*-attentive (50% of trials) than attentive conspecific (21%), or when viewing the stimulus while alone (21%). No hunching behaviour was observed.

Table 8.2: Results for GLMM analyses of the distribution of communicator behaviours across the '*Communicator Alone*', '*Experimental-Away*' and '*Experimental-Towards*' conditions.

Behaviour	Fixed effects	Estimate	Std. Error	Z-value	P
Stimulus directional	Communciator Alone	-1.02	1.05	0.97	0.332
	Experimental-Away	1.01	0.98	1.03	0.303
	Experimental-Towards	1.18	1.08	1.09	0.278
Locomotory directional	Communciator Alone	-1.57	0.81	1.94	0.053
	Experimental-Away	8.64	0.92	0.94	0.350
	Experimental-Towards	-7.81	1.00	0.00	0.999
Non-stimulus directional	Communciator Alone	-0.98	0.64	1.54	0.124
	Experimental-Away	1.61	0.83	1.95	0.051
	Experimental-Towards	0.98	0.81	1.21	0.225
Auditory	Communciator Alone	-2.52	1.04	-0.47	0.999
	Experimental-Away	-1.05	1.47	1.01	0.403
	Experimental-Towards	-1.70	0.47	0.00	0.999
Multimodal	Communciator Alone	-2.52	1.04	-0.47	0.999
	Experimental-Away	-1.05	1.47	1.01	0.403
	Experimental-Towards	-1.70	0.47	0.00	0.999

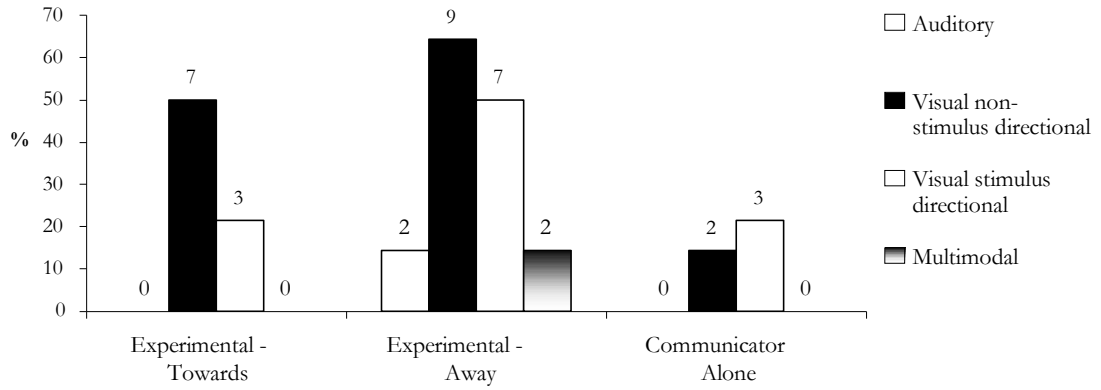


Figure 8.1: Communicator behaviour. Percent '*Experimental-Towards*' (N=14), '*Experimental-Away*' (N=14) and '*Communicator Alone*' (N=14) trials, where communicators produced auditory, visual non-stimulus directional, visual stimulus directional and multimodal behaviours.

Gaze behaviour: Fifty percent (14 of 28) of *experimental* trials could be reliably scored for gaze changes. The target conspecific's back was turned to the communicator throughout three of these trials, which were therefore excluded from an analysis of potentially communicative gaze behaviour. Communicators were no more likely than chance to look referentially to the conspecific (look to the conspecific within 2s of looking away from the stimulus, while being within the conspecific's 'open'/'peripheral' field of vision; 72.73%, 8 of 11 of trials, Binomial test: n = 11, p = 0.227), nor to shift gaze from the stimulus to the conspecific (within 2s of looking away from the stimulus) and back to the stimulus (within 2s of looking away from the conspecific), while being within the conspecific's 'open'/'peripheral' field of vision (45.45%, 5 of 11 trials, Binomial test: n = 11, p = 1). Communicators produced an auditory cue in two of 28 *experimental* trials, both while in the presence of a non-attentive conspecific, and in both cases auditory behaviour were followed by gaze alternation between the stimulus and conspecific, while being in conspecific's 'open' visual field. In both cases, targets co-oriented looked to the stimulus location (Figures 8.2 and 8.3).

Figure 8.2: '*Experimental–Away*' condition; From left: (1) The communicator (left, who had viewed the stimulus in a previous trial) views the stimulus (encircled). (2) The communicator abruptly and noisily scrambles up wired rubber structure, vigorously shaking a hanging tyre in the process. (3) Target (right, the communicator's mother) turns and looks towards the communicator, who looks to the stimulus area, then target, and back to the stimulus area.

Figure 8.3: '*Experimental–Away*' condition. From left: (1) The Communicator views stimulus, (2) bangs hand on door by stimulus, (3) turns to look to the experimenter, then target conspecific (4), who turns around. When the target has turned, the communicator looks back to the stimulus.

8.3.2 Communicator behaviours leading targets to look to the stimulus area

None of the recorded behaviours that communicators produced during the stimulus phase of experimental trials where they viewed the stimulus while in the presence of an attentive (Table 8.2, Figure 8.4) or non-attentive conspecific (Table 8.3, Figure 8.5) significantly affected whether or not targets looked to the stimulus area.

Table 8.2: Significance table. GLMM test for a difference in the probability that targets looked to the stimulus area when communicators produced various behaviours while viewing the stimulus in the presence of an attentive conspecific ('*Experimental-Towards*' condition).

Fixed effects	**Estimate**	**Std. Error**	**Z-value**	***P***
Intercept	-2.31	1.33	0.10	0.999
Stimulus directional	2.30	2.32	0.90	0.788
Locomotory stimulus directional	-1.23	1.42	0.70	0.871
Auditory	4.01	3.41	0.00	1.000
Non-stimulus directional	3.01	2.51	0.00	1.000

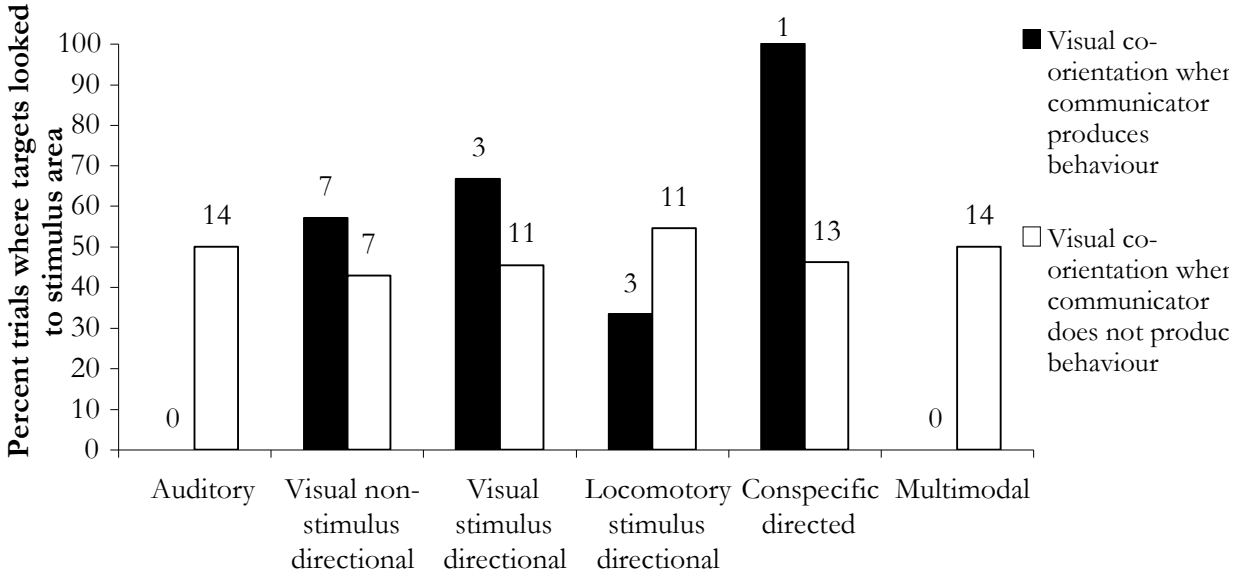


Figure 8.4: Attentive targets' looks to stimulus area as a function of communicator behaviours. Percentage of conspecific looks to the stimulus area during '*Experimental-Towards*' trials (N=14) when communicators did/did not produce various cues. Labels above columns indicate the number of trials in which communicators did/did not produce the behaviours on which the percentage is based.

Table 8.3: Significance table. GLMM test for a difference in the probability that targets looked to the stimulus area when communicators produced various behaviours while viewing the stimulus in the presence of a non-attentive conspecific ('*Experimental-Away*' condition).

Fixed effects	**Estimate**	**Std. Error**	**Z-value**	***P***
Intercept	-2.10	3.35	0.10	0.999
Stimulus directional	1.32	2.28	0.00	1.000
Locomotory stimulus directional	-1.07	3.00	0.10	1.000
Auditory	4.14	3.33	0.00	1.000
Non-stimulus directional	3.22	2.35	0.00	1.000

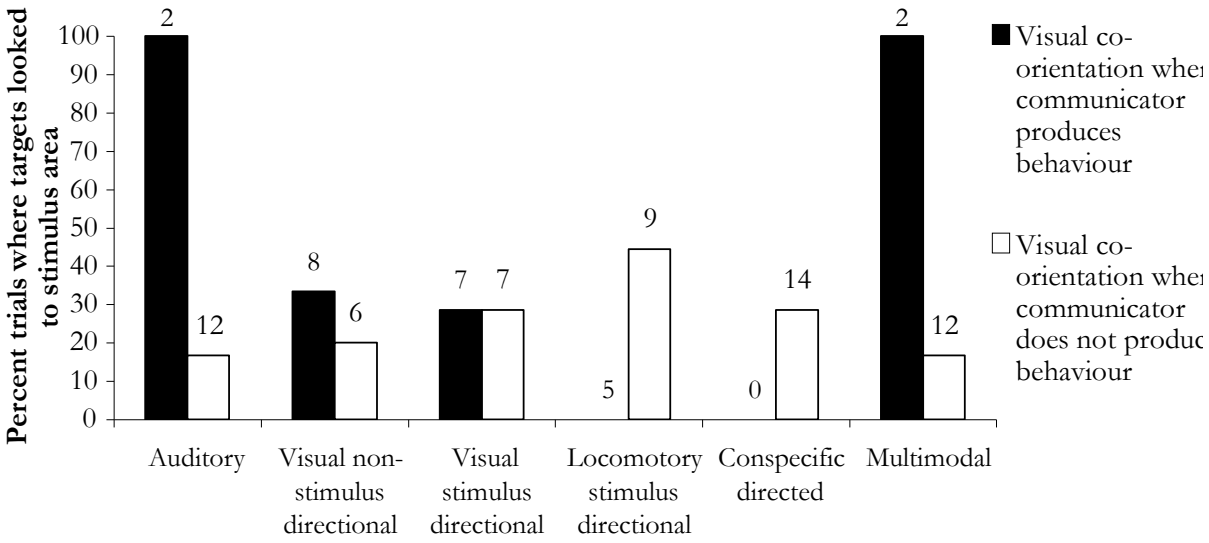
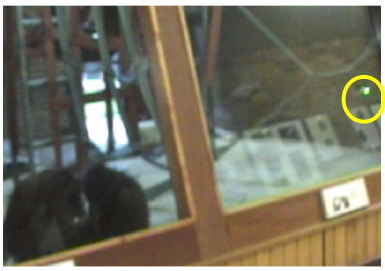


Figure 8.5: Non-attentive targets' looks to stimulus area as a function of communicator behaviours. Percentage of conspecific looks to the stimulus area during '*Experimental-Away*' trials (N=14) when communicators did/did not produce various behaviours. Labels above columns indicate the number of trials in which communicators did/did not produce the behaviours on which the percentage is based.

8.3.3 Qualitative analysis of communicator target interactions

Some trials contained interesting gaze interactions between communicators and targets that did not lend themselves to quantitative analysis, given the rarity with which they occurred. While the observations remain anecdotal, they suggest that, although statistically non-significant when all individuals and dyad constellations were analysed, some individuals may have used gaze communicatively to convey something about the stimulus. This seems to have particularly been the case in mother-offspring dyads interactions, for which several trials included repeated communicator gaze alternation, while being within the conspecific's 'open' or 'peripheral' field of vision. Some of these trials are described in Figure 8.2, and Figures 8.6, 8.8 and 8.9, below.

Pre-stimulus display phase.

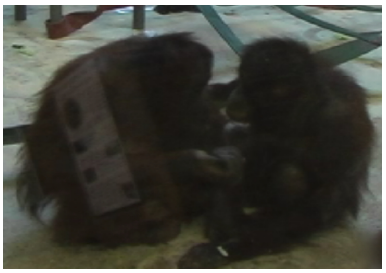


Stimulus displayed.

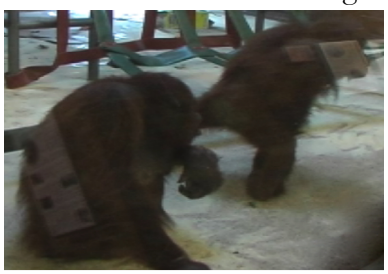
Communicator looks to stimulus.

Communicator looks to target.

Communicator looks to stimulus.



Communicator looks to target.



Target turns and looks to stimulus location.

Target looks back to communicator.

Target looks to stimulus location.

Figure 8.6: '*Experimental-Towards*' trial involving gaze alternation. Repeated gaze alternation between the stimulus and target by the communicator (left), followed by visual co-orientation and 'checking' behaviour by the target upon finding nothing at the focus point of the communicator's attention.

Figure 8.7: '*Experimental-Away*' trial. From left: (1) Communicator looks to stimulus (encircled), (2) looks to the experimenter, (3) approaches stimulus, (4) which makes target (encircled) turn and look to communicator. The communicator then looks to stimulus, then to target, and then back to stimulus, while being within target's 'open' field of vision. Target does not approach to look to the stimulus.

Figure 8.8: '*Experimental-Towards*' trial. From left: (1) Stimulus displayed. (2) Communicator (left) sees stimulus, and (3) looks to infant (right, who looks to mother and stimulus), and back to the stimulus, and then approaches the stimulus.

Figure 8.9: '*Experimental-Towards*' trial. From left: (1) Pre-stimulus phase. (2) Communicator (right) sees stimulus. (3) Communicator looks to experimenter, and alternates gaze between the experimenter, stimulus and possibly target 7 times within the following 10s (laser pointer is disguised, and only the stimulus point on the grass should be visible to the communicator). Target (left) is immediately in front of the communicator, precluding unequivocal determination, as to whether the communicator also looks to target while looking to the stimulus. Target appears to notice the communicator's movements, and turns and scans over the stimulus area, and upon finding nothing, looks back to communicator and, within 2s thereafter, to stimulus area again.

8.4 Discussion

Contrary to prediction orangutans were no more likely to produce auditory, locomotory and visual stimulus directional cues when they viewed the stimulus in the presence of an attentive or non-attentive conspecific, than alone. Moreover, none of the recorded behaviours consistently triggered conspecific attention following to the stimulus location. There was also no individually consistent, nor species-wide, evidence of active attention manipulation, in the form of multimodal behaviours (i.e., sequential auditory and visual stimulus directional behaviours).

Overall, this supports the results of Chapter 7 (Orangutan Attention Following), which suggested that the orangutans did not actively attract the attention of non-attending conspecifics to the stimulus location, and that conspecific re-orientation to the stimulus area occurred on the basis of adventitious cues emitted by individuals viewing the stimulus. More specifically, conspecifics were only significantly more likely to look to the stimulus area when they faced towards communicators during the stimulus projection and needed only read the communicators' adventitious attentional cues, and turn around, so as to look to the stimulus (i.e., when visual co-orientation required no communicative efforts on the part of the communicator).

Nonetheless, in two cases, individuals (the adult male and a juvenile female viewing the stimulus in the presence of its mother) followed an auditory behaviour by a stimulus directional behaviour. In both cases, the animals viewed the stimulus in the presence of a non-attentive conspecific and followed the sequential auditory-stimulus-directional behaviour by gaze shifts between the stimulus and conspecific, who co-oriented to the stimulus area. Moreover, while statistically non-significant, there was a clear tend for communicators to produce visual stimulus directional as well as visual *non*-stimulus directional behaviours more frequently when viewing the stimulus in the presence of a *non*-attentive than an attentive conspecific or alone. Despite neither of these behavioural classes reaching statistical significance when analysed individually and on a group-wide basis, it seems that the orangutans' behavioural responses to the stimulus were, overall, stronger when it was viewed in the presence of a non-attentive conspecific. While this might be explained with reference to potential differences in arousal levels when viewing ambiguous stimuli in the presence of a non-attentive rather than attentive conspecific, arousal levels should, theoretically, be even higher when the animals viewed the stimulus while alone. Interestingly, both the chimpanzee and the bonobo populations tested were also more likely to produce stimulus directional behaviours when they viewed the stimulus in the presence of a

non-attentive than attentive conspecific or alone. Overall, the orangutans seemingly stronger behavioural responses to the stimulus when in the presence of a non-attentive conspecific suggests that some of the orangutans may have increased their responses to the stimulus (and potentially, communicative efforts) when there was little chance conspecifics might detect the stimulus on their own.

In accordance with a comprehensive observational study of orangutan intra-specific communication, which found a complete absence of auditory signals (Liebal *et al.* 2006), no vocal signals were observed, and only two trials included auditory cues. In contrast, orangutans frequently produce auditory signals in experimental studies, to solicit human attention (Poss *et al.* 2006; Cartmill & Byrne 2007), and use a number of gestures in experimental settings that are not used as intentional gestures during interactions with conspecifics (Poss *et al.* 006; Zimmermann *et al.* 2009; Cartmill, E. *pers. com.*). Orangutans may simply use a different collection of signals to attract and direct the attention of experimenters and keepers than conspecifics.

While previous research has demonstrated that orangutans discriminate between the different states of visual attention in others, view others as agents capable of having intentions and perceptions, and have some understanding of the effectiveness of their own signals, which they use appropriately to gain others' attention in imperative contexts (Call & Tomasello 1994, 1998; Shillito *et al.* 2005; Poss *et al.* 2006; Liebal *et al.* 2006; Cartmill & Byrne 2007; Genty & Byrne 2009; Genty *et al.* 2009), the present results provide little evidence that the orangutans, as a group, behaved differently as a function of conspecifics' visual attention, or communicated about the stimulus. This may be interpreted to suggest that (i) orangutans may communicate intentionally about distal objects to humans, but not conspecifics, and that orangutans trained to point (though not experimentally naïve orangutans) may extend this behaviour to point for conspecifics, (ii) that the visual stimulus had a lower motivational value than the food that has evoked intentional communication in other experimental paradigms, and/or (iii) that orangutans may communicate imperatively about distal objects they desire but not declaratively (or social referentially) about a non-food object predicted to evoke interest rather than want.

Do orangutans use gaze as an intentional referential signal?

To examine de Waal's (2001) suggestion that apes may intentionally use gaze as a referential signal, I examined the orangutans gaze behaviour with specific emphasis on the few trials, in which they produced auditory cues, so as to separate referential looking ('stimulus–conspecific' gaze behaviour), from intentionally communicative instances. Communicators were

no more likely than chance to look referentially to the target conspecific, nor to shift gaze from the stimulus to the conspecific (within 2s of looking away from the stimulus) and back to the stimulus (within 2s of looking away from the conspecific), while being within the conspecific's 'open' or 'peripheral' field of vision. While statistically non-significant when all individuals and dyad constellations were analysed, the results, however, suggest that some individuals may have used gaze communicatively to convey *something* about the stimulus. In particular, the only two trials, in which communicators preceded an auditory cue (both while in the presence of a non-attentive conspecific), lend support to this notion. In both cases auditory cues were followed by gaze alternation between the stimulus and conspecific ('stimulus-conspecific-stimulus' gaze behaviour) while being in conspecific's 'open' visual field, and in both cases the conspecific turned around to look to the stimulus location. Moreover, one trial involved a mother repeatedly alternating gaze between the stimulus and her attentive juvenile daughter, which was followed by visual co-orientation to the stimulus location and checking behaviour by the daughter ('stimulus area – mother – stimulus area' gaze behaviour).

Conspecifics' looks to the stimulus area were randomly distributed across trials, in which communicators did and did not look referentially to the conspecific or shifted gaze between the stimulus, target and back to the stimulus, while being within a conspecifics' 'open' or 'peripheral' field of vision. While this gaze behaviour failed to trigger attention following, this may be partially explained by the low statistical power afforded by the limited number of trials, in which orangutan communicators produced these behaviours. Moreover, given that trials were performed opportunistically and dyad compositions not controlled, the finer gradations and influence of conspecific relationship on attention co-ordinating behaviours remain untested.

Furthermore, in one experimental trial (detailed in Figure 8.3) the communicator banged on the door, on which the stimulus was displayed, and before turning to look to a conspecific behind itself, looked to me, the experimenter. In another trial, the same communicator (the adult male) also looked to me, before looking to its conspecific and then back to the stimulus (trial detailed in Figure 8.7). It is possible that, despite meticulous care exercised to prevent the animals detecting the origin of the stimulus (and grasping the nature of the experiment), that (some of) the animal(s) may have done just that. If so, the stimulus' value as a novel, interesting object of uncertain origin, may have been reduced to simply 'another odd thing that happens around people', with little need to engage a conspecific. An alternative interpretation of the communicator's behaviour in these two trials, is that the animal might not have grasped the origin of the stimulus, but simply that the physically closest other individual, with whom to

socially reference, was a human (i.e., the experimenter), and that looks to and engagement with a conspecific were unnecessary.

Given orangutans semi-solitary existence, one might predict that visual, and particularly gaze-related, communication play a lesser role for orangutans than other great apes species (Delgado & Van Schaik 2000). While the overall results suggest that the orangutans did not use locomotion or gestures to actively bring about instances of joint attention, a few interactions suggest that the species may use more subtle, less dynamic behaviours (including gaze behaviours) that effectively coordinate others' to the focus of their own attention. Thus, while, there was no overall evidence that orangutans directed others' attention to the stimulus, the behaviour of some individuals was consistent with the suggestion that apes may use gaze and gaze alternation as ostensive (Menzel 1973, 1974; Gómez 1990, 1991) and referential signals (de Waal 2001).

CHAPTER 9: General discussion

9.1 Introduction

The thesis now turns to the discussion, further elaboration and contextualisation of the research presented in the previous chapters. The key findings are summarised, and the performance of the three species compared, and empirical and theoretical implications of the findings are discussed. A number of methodological strengths and limitations within this program of research are discussed and finally, suggestions for future studies, which will expand on the present research program, are proposed.

9.2 Empirical findings

9.2.1 Summary of key findings

The principal aims of this thesis were to (i) investigate the conspecific attention following skills of three species of non-human apes, and (ii) devise a methodological approach to test if the apes would lead conspecifics to detect a novel stimulus, that would allow a distinction of adventitious and intentionally emitted cues. An extensive battery of controls was devised, to explore if the animals considered the presence and visual attention of conspecifics when viewing a novel stimulus, as well as the probability of conspecifics detecting the stimulus on their own and by chance. A further key aim was to (iii) identify potential behaviours that consistently function as cues triggering intra-specific attention following, and test if the apes took conspecific presence attention into consideration when engaging in such behaviours, including potentially, directional signalling that, while not necessarily corresponding to hand-pointing, might be meaningful to the animals.

In Chapter 2, I described the general methodology used with the three species and reported the attentional responses of chimpanzees to the behaviour of ten adult and three infant conspecifics shown a novel laser stimulus. Adult chimpanzees failed one control condition (which nonetheless showed the right tendency), involving comparison of initially non-attentive targets' looks to the stimulus location during the 30s that the stimulus was shown, and the

preceding 30s when it was not. Nonetheless, they passed all other control conditions and were more likely to look the stimulus area when a communicator viewed the stimulus, than in the absence of a communicator or the presence of a communicator ignorant as to the presence of the stimulus, and in the absence of the stimulus, while orienting either towards or away from the communicator. Three infant communicators received a limited number of conditions, but consistently brought about conspecific co-orientation to the stimulus area. The study involved only three trials where infants served as both targets and communicators, yet, infants co-oriented to communicator attention in all trials, suggesting that they readily followed conspecific attentional cues. This is consistent with a finding that one chimpanzee (with extensive experimental experience) reliably followed the head orientation of a human experimenter to a location behind itself by 20 months of age (Okamoto *et al.* 2004), and adds to this, by suggesting that experimentally naïve infant chimpanzees also co-orient to conspecific (versus human) attention to locations where no events may be expected to occur (wall vs. the infant's mother: Okamoto *et al.* 2004). Conspecifics, however, emitted cues other than only head cues, and often approached and inspected the stimulus, thus providing far more conspicuous cues to the location of the stimulus, than the head cues provided in the experiment involving a human experimenter/communicator (Okamoto *et al.* 2004). Overall, the results suggest that the infant as adult chimpanzees consistently brought about conspecific co-orientation when presented with a novel/interesting visual stimulus, and indeed that both infant and adults followed the attention of conspecifics.

A key finding in Chapter 3 was the identification of a behavioural component, 'hunching', which when included, consistently led the chimpanzee to co-orient to the communicator's attentional focus. The component consisted of the chimpanzee rounding its back, tilting its body forward, drawing the head into its shoulders and pushing its chin forward towards the focus of its attention. A similar 'hunching' component has been reported in quadrupedal, bipedal and sitting positions in multiple contexts among wild chimpanzees (see e.g., Nishida *et al.* 1999), but never identified as a potential component of a form of functional or intentional chimpanzee attention re-direction. It is plausible that through a statistical contingency and its occurrence in greeting, aggression and courtship contexts, the behaviour has acquired a function of adventitiously signalling intense attention towards a social entity, onto which some behaviour will follow. There was, however, a clear trend for the chimpanzees to selectively adopt the 'hunching' posture when they viewed the stimulus in the presence of a conspecific rather than alone (the comparison was statistically non-significant, but very closely approached significance [$p = 0.056$]), and they never assumed the posture in control conditions

where they did not view the stimulus. Moreover, in all cases where chimpanzees adopted the posture while viewing the stimulus in the presence of a *non*-attentive conspecific, it was preceded by an auditory behaviour. Overall, the results suggest that the behaviour may represent a case of a naturally occurring (albeit rarely deployed) intentional, declarative-like behaviour. In Chapter 4, I analysed naturally occurring attention following episodes, of which four included the 'hunching' posture, thus demonstrating that the behaviour occurs in contexts other than that of potentially laser-stimulus-induced increased arousal in the experimental manipulation. Overall, the results go some way to suggest that the behaviour may have been produced intentionally and referentially.

In Chapter 4, I also applied Chance's (1967) 'Social Attention Hypothesis' (that individuals accord and receive attention as a function of dominance rank) to attention *following,* and found that the chimpanzees were more likely to follow the attention of the alpha male, who was less likely to follow the attention of others. While the 'Social Attention Hypothesis' is traditionally tested using e.g., 'point sampling' to measure the frequency of looks to conspecifics, attention following is a plausible extension of the predictions made by the hypothesis. The results represent the first of their kind, and add to the body of evidence, suggesting that the attention structure of primates (e.g., wild baboons, patas monkeys and possibly orangutans) is based on social dominance (Kummer & Kurt 1963; McNelis & Boatright-Horowitz 1998; Kaplan & Rogers 2001).

In Chapters 5 and 6, I described an adaptation of the general method to a bonobo population, who, like the chimpanzees, followed conspecific attention to the stimulus. Unlike the chimpanzees, the bonobos also consistently followed conspecific attention when the setup required that they first locomote around a visual obstacle. This effect was, however, only statistically significant when only the first trial that subjects received was included in the analysis (and not when all trials that individuals received were analysed jointly). This was possibly because the novelty value of the stimulus decreased after repeated exposures, where communicators were allowed to examine the stimulus for up to 30s, and thus the strength of their responses and potential interest in directing others to the stimulus (for e.g., potential social referencing purposes) diminished. None the behaviours that the bonobos produced upon viewing the stimulus significantly predicted whether conspecifics looked to the stimulus area, however, like the chimpanzees, they intriguingly preferentially produced visual stimulus directional cues when viewing the stimulus in the presence of a *non*-attentive conspecific.

In Chapters 7 and 8, I reported the results for orangutans, who, overall, followed the

attention of conspecifics, but neither showed evidence of geometric attention following, nor of selective production of stimulus directional cues when viewing the stimulus in the presence of conspecific.

9.2.2 Species comparison

This section provides a brief comparison of the behaviour of the three species (including direct statistical assessment of key behaviours).

9.2.2.1 Attention following

Although the stimulus was removed immediately before it was detected, individuals of all three species looked longer towards the stimulus area during the stimulus than pre-stimulus phase of experimental trials, suggesting an expectation of a point of interest. Overall, all the three species co-oriented to the stimulus when facing a conspecific viewing it. Bonobo targets were, however, statistically more likely than both chimpanzees and orangutans to look to the stimulus area during the 30s of experimental trials that the stimulus was shown to a conspecific than the preceding 30s when it was not (GLMM with 'phase' and 'species' entered as factors and participant as a random factor: Bonobos: Est. = 5.2, SE = 0.90, z = 5.81, p = 0.000; Chimpanzees: Est. = 0.18, SE = 0.43, z = 0.42, p = 0.676; Orangutans: Est. = 0.16, SE = 0.46, z = 0.349, p = 0.727). This apparent species difference appears to have been a 'true' difference, as the bonobos received a higher proportion of experimental trials that required conspecifics to follow communicators' attention under unfavourable geometric conditions that required them to first locomote around a visual barrier (thus reducing the probability of adventitious stimulus detection, due to scanning or simply movement (proportions of experimental trials requiring geometrical attention following: Bonobos: 82%, Chimpanzees: 41%, Orangutans: 43%). Given the small proportion of geometrical attention following trials that the chimpanzees and orangutans received, no direct tests of the three species' performance on this type of trials was conducted. Bonobos, however, consistently followed conspecific attention geometrically.

There was no evidence that bonobo communicators produced more salient cues, as to the focus of their attention. Thus, this apparent species difference in readiness to follow conspecific attention, suggest that either the bonobos were more interested in the attention of conspecifics than members of the other two species tested, or the bonobos were more motivated to move and locomote in order to co-orient to others' focus of attention, possibly underscored by the species', seemingly overall, more 'active' way of life.

9.2.2.2 Attentional cues

Overall, all three species seemed to show stronger behavioural responses to the stimulus when viewing it in the presence of a *non*-attentive conspecific (see Figures 3.5, 6.4 and 8.1 for the behaviours that the three species, respectively, produced across the three main conditions). Likewise, interestingly, both chimpanzees and bonobos preferentially produced visual stimulus directional behaviours when viewing the stimulus in the presence of a non-attentive conspecific. Some individuals of these species consistently and selectively preceded stimulus directional behaviours by an auditory behaviour when viewing the stimulus in the presence of a non-attentive conspecific, suggesting that the individuals may have considered conspecific presence and visual attention. Nonetheless, given that all three species produced a higher proportion of stimulus directional behaviours (and in the case of orangutans, visual *non*-stimulus directional behaviours[49]) when viewing the stimulus in the presence of a non-attentive conspecific, it may simply be that the apes increased their overall responses to the stimulus (and potentially, communicative efforts, without resorting to auditory behaviours) when there was little chance conspecifics might detect the stimulus on their own.

There was no species-wide evidence for active attention calling in any of the species, although the chimpanzees were more than three times as likely to produce an auditory behaviour when viewing the stimulus in the presence of a non-attentive conspecific, and six times more likely to do so than when they viewed the stimulus on their own. Nor was there any species-wide evidence of sequential auditory and stimulus directional behaviours for any of the species tested, yet there were, particularly for the chimpanzees, noticeable individual differences; Some individuals consistently followed an auditory behaviour by a stimulus directional behaviour only when viewing the stimulus in the presence of a non-attentive conspecific, and reliably lead conspecifics' attention to the stimulus location.

Contrary to previous studies, which have found no evidence that apes actively call the attention of non-attending human experimenters (in a food begging experiment) and conspecifics (based on a 75 hour observational study of chimpanzees) before producing a more specific visual cue, but tend to locomote into the visual field of a desired recipient (Liebal *et al.* 2004a,b), some of the chimpanzees and bonobos in the present experiment consistently attracted the attention of non-attending conspecifics by means of auditory behaviours, before

[49] The selective production of this behaviour when orangutans viewed the stimulus in the presence of a non-attentive conspecific was non-significant, yet closely approached significance ($p = 0.051$).

adopting a stimulus directional behaviour (and did so only when viewing the stimulus in the presence of a non-attentive conspecific).

Chimpanzees showed a strong trend to produce a stimulus directional 'hunching' behaviour when viewing the stimulus in the presence of a conspecific rather than alone (the effect was statistically non-significant but closely approached significance [p=0.056]), while this behaviour was never observed in any of the trials involving bonobos and orangutans. Moreover, in all cases where chimpanzees adopted the posture, while viewing the stimulus in the presence of a *non*-attentive conspecific, it was preceded by an auditory behaviour. The posture may represent a naturally occurring (albeit very rarely deployed) intentional, declarative-like behaviour.

The most distant human relative studied, orangutans, showed few signs of actively calling and re-directing conspecific attention, and neither showed individually consistent, nor species-wide evidence of active attention manipulation, stimulus directional behaviours, or multimodal communication. Indeed, associations between the orangutans' responses to the stimulus and conspecifics' looks to the stimulus area were conspicuous by their absence. It is frequently argued that the social communication of the evolutionary line leading to *Pan* and *Homo* may have become increasingly sophisticated since the split from the ancestor shared with orangutans 10-12 m.y.a., and indeed, that the social communication of orangutans is less sophisticated than that of the *Pan* species (e.g., Bennett 1998, cited by Liebal *et al.* 2006). It is, however, likely that orangutans' poorer performance in a number of experimental paradigms may owe to motivational factors, rather than cognitive and communicative capabilities. Anecdotally, orangutan mother-offspring dyad interactions in the present experiment contained a number of cases of e.g., repeated communicator gaze alternation and consequent conspecific looks to the stimulus area, and of auditory behaviours followed by gaze alternation between the stimulus and the communicator's mother or offspring. While only anecdotes, these observations emphasise three things: (i) the importance of the social relationships of interlocutors on the nature of the communication; orangutans are most likely *more* likely to engage in triadic interactions with individuals, with whom they are emotionally close (as in the case of e.g., mother-offspring dyads); (ii) individual differences may be related to particular life-history periods, such as those that – in the apes' natural habitats – would entail more frequent and intense social interactions and be under selective pressure for closer social attention (i.e., the infant and juvenile stages, and thus, by implication, again mother-offspring interactions; and (iii) while orangutans engage in triadic interactions with conspecifics (see e.g., Pitman & Shumaker

2009), their social communication may involve more subtle and less action-based behaviours than that of the (seemingly overall more motile) *Pan* species, thus making such behaviours less conspicuous. The implication is that care should be exercised when attributing socio-cognitive performance to species differences, without careful consideration of ontogeny and motivational factors, and indeed individual differences (and consequently the potential problem of testing relatively small sample sizes).

There was no overall statistically significant evidence that the three species used gaze shifts as an ostensive signal to secure and direct others' attention, however the behaviour of some animals was consistent with the suggestion that apes may use gaze and gaze alternation as ostensive (Menzel 1973, 1974; Gómez 1990, 1991; O'Connell 1994) and intentionally referential signals (de Waal 2001). In all species, communicators shifted gaze from the stimulus to the conspecific and back to the stimulus while being within the conspecific's 'open' or 'peripheral' field of vision in 50% or more of trials where gaze behaviour could reliably be coded (chimpanzees: 60% [14 of 23 trials], bonobos: 50% [14 of 28], orangutans: 72% [8 of 11]). Moreover, analysis of 45 naturally occurring attention following episodes (see Chapter 4), showed that in 24% (11 of 45) chimpanzee targets alternated gaze between the communicator and the communicator's focus of attention, and back to the communicator. While none of these behaviours reached statistical significance, they suggest that individuals may have had some awareness that conspecifics were in some way connected to object of their attention.

9.3 Methodological issues

9.3.1 Strengths

Previous studies of conspecific gaze following in apes have included controls that have used a control condition similar to the '*Target Alone*' control deployed the present design ("no conspecific present in the immediate vicinity of the subject": Tomasello *et al.* 1998, p. 1065), or have used a version of the '*No Stimulus*' control, in which a human either held up an empty hand ('*No Stimulus*' condition: Pitman & Shumaker 2009) or an object ('*Experimental*' condition: Ibid.). The absence and design of key controls in these studies, however, opens the possibility for 'low level' explanations underlying the observed visual co-orientation. For example, eliminating the possibility that conspecific presence increases the scanning frequency, and consequently accidental stimulus detection by target animals, requires inclusion of a control where the

stimulus is consistently presented outside the view of target animals, while in the presence of a conspecific ignorant as to the presence of the stimulus (i.e., a consistent implementation of the '*Target and ignorant communicator*' control; multiple targets critique).[50]

In contrast to the two studies of conspecific gaze following (Tomasello *et al.* 1998; Pitman & Shumaker 2009), the present design did not require target animals to re-orient to points where interesting events, such as human presence, frequently occurred (interesting events critique). While such presence does not raise question, as to the animals' demonstrated gaze following, it may increase readiness to co-orient on the basis of observed adventitious cues emitted by conspecifics. Indeed, this suggestion receives some support from findings that, while one infant chimpanzee followed human gaze and pointing cues to a target located next to its mother, behind the infant's back (i.e., potentially interesting event: Okamoto-Barth & Tomonaga 2006), Tomasello and colleagues (Tomasello *et al.* 2001) found no evidence that infants followed human gaze cues to a point at the ceiling outside the infants' own visual field (i.e., no expectation of an interesting event).

In both of these studies (Tomasello *et al.* 1998; Pitman & Shumaker 2009) social group sizes ranged from two to seven individuals, with several conspecifics viewing and providing cues as to the location of the stimulus. The inclusion of several individuals as communicators precludes conclusions as to whether targets reacted to the attentional cues of one or several individuals, and viewing multiple individuals sharing a visual referent may reduce the threshold for initiation of automatic visual co-orientation (multiple communicators critique). In contrast, the experiment reported in this thesis entailed that only one individual served as the 'communicator'.

Tomasello and colleagues did also not examine target looks to the stimulus area while in the presence of a conspecific but absence of the stimulus (controlled in the present experiment by means of the '*No Stimulus*' control and the '*Pre vs. Post*' control, comparing target looks to the stimulus area prior to and during the presentation of the stimulus). Instead, the studies by Tomasello and colleagues compared only target animals' looking behaviour across the stimulus phase of *experimental* trials and the equivalent of the stimulus phase of the '*Target Alone*' control deployed in the current experiment. As the experimental pre-stimulus phase, in the present

[50] In the design deployed in this thesis, all subjects received at least two '*Target and Ignorant Communicator*' trials per trial sequence, and for some subjects (who could not be tested alone) the '*Target Alone*' control trial was exchanged for an additional '*Target and Ignorant Communicator*' control trial.

experiment, seemed to evoke somewhat higher proportions of target conspecific looks to the stimulus location than the stimulus phases of either of the control conditions, it is likely that pre-stimulus vs. stimulus phase control yields slightly different information. This type of control ('*pre versus post*') does not seem to have been included in previous studies of neither child nor non-human primate studies of attention following, but seems to represent a more conservative baseline measure (i.e., it produces slightly higher looks to the stimulus location than the other control conditions), and thus represents a crucial measure for comparison to be included in future gaze following studies.

9.3.2 Limitations

There were a number of limitations to the design and data collection and consequently the ability draw unequivocal conclusions from the data. First, subject dyads were not pre-selected, but chosen opportunistically. While dyad pre-selection, involving permutations of a subordinate communicator and dominant target (and *vice versa*) is preferable for a comparison of the effect of rank relationships (in light of evidence that readiness to follow others' attention is coloured by social dominance in chimpanzees, see Chapter 4), this was unfeasible due to the rarity of favourable inter-animal constellations and the preferred interactions and locations of the animals.

A second limitation was that the species received different proportions of trials that required conspecifics to 'only turn' or first 'locomote' around a barrier to co-orient to the communicator's attention ('direct' and geometric attention following; Percentage experimental geometric attention following trials: chimpanzees: 41%, bonobos: 82%, orangutans: 43%). While orangutans did not co-orient to communicators' attention in any geometric attention following trials (suggesting that the effect represents a genuine species difference, rather than being an artefact of the design), the study would have benefited from an even proportion of *turn* and *locomote* trials, to ensure that species differences between the *Pan* species were not masked (e.g., at species level, bonobos passed all control conditions involving geometric attention following trials [based on the first 'locomote' trial that subjects received in the various conditions], while chimpanzees failed all).

A third limitation was that the design did not control for the possibility that the permutation of an arousing stimulus and conspecific presence accounted for different communicator behaviour in experimental trials versus trials, in which communicators viewed

the stimulus while alone. If, however, cues emitted by communicators were caused by only increased arousal levels related to conspecific presence, one might predict an positive association between the production of noticeable cues and 'degree' of conspecific attention, i.e., a larger proportion of noticeable behaviours produced when communicators viewed the stimulus in the presence of an attending than non-attending conspecific or alone (i.e., '*Experimental-facing towards*' > '*Experimental-facing away*' > '*Communicator Alone*'). In contrast, chimpanzees and bonobos showed an (albeit statistically non-significant) increasing trend towards producing auditory, visual stimulus directional and visual non-stimulus directional behaviours in a larger proportion of trials when they viewed the stimulus in the presence of a *non*-attending conspecific, than either alone, or in the presence of a conspecific facing them (i.e., '*Experimental-facing away*' > '*Experimental-facing towards*'/'*Communicator Alone*'). This suggests that rather than reflecting merely arousal levels, the difference in cue production may have reflected a consideration of conspecific attention, and perhaps an attempt to secure conspecific attention to (minimally) self, which was more vigorous when conspecifics were non-attentive than attentive.

9.4 Ape communication and joint attention

The study of similar abilities in closely related species, allows one to ascertain homologies (i.e., shared evolutionary ancestry), as abilities, motivations and signals shared by closely related species are likely to have been present in their last common ancestor. There has been some suggestion that bonobos may have a greater language-like ability in the vocal domain than chimpanzees (de Waal 1988; Hopkins & Savage-Rumbaugh 1991; Taglialatela *et al.* 2003) and some studies (Pollick and de Waal 2007; though not all, see Pika *et al.* 2005) suggest that they use gestures more flexibly than chimpanzees (i.e., use gestures less consistently within specific contexts). Curiously, while a comparative study of *Pan* communication suggested that chimpanzees were more likely to engage in multimodal communication than bonobos, the multimodal cues of bonobos were found to be more effective than gestures alone, in eliciting a response from a conspecific, while this was not the case for chimpanzees (Pollick & de Waal 2007). Bonobos' high responsiveness to combinatorial signalling led to the suggestion that, despite the genetic equidistance of the *Pan* species to humans, bonobos may represent a better model of the symbolic communication of early human ancestors. The present results do not immediately support this; Chimpanzees' multimodal cues were effective in eliciting conspecific co-orientation to the stimulus location, while this was not the case for bonobos. This species

difference may, however, partly have been caused by the small number of trials, in which bonobos combined auditory and visual stimulus directional behaviours. Moreover, the study by Pollick and de Waal (2007) included differentiation between three facial expressions ('relaxed open mouth', 'silent bared teeth', 'silent pout face'), which may have influenced the discrepancy of the results of that and the present study. There was, in the present study nonetheless, some suggestion that bonobos were more attentive to conspecific behaviour than chimpanzees.

There is considerable evidence that captive apes engage in imperative communication with humans (e.g., Leavens & Hopkins 1999; Leavens *et al.* 2009; Zimmermann e*t al.* 2009), and although few, there are reported instances of intra-specific imperative pointing gestures among orangutans (Pele *et al.* 2009) and chimpanzees (Savage-Rumbaugh 1986; Pika & Mitani 2006). Structurally and functionally, these pointing behaviours are good approximations of human pointing, although they mostly include the whole hand, and no index-finger-extension (Leavens & Hopkins 1999). Considerable evidence (for a recent review, see Leavens & Racine 2009), including that presented in this thesis, suggests that apes engage in joint attention behaviours, such as attention following, gaze alternation and some form of 'pointing'. While this no longer seems controversial, it is widely argued that the joint attention behaviours of humans and great apes are qualitatively different (e.g., Povinelli *et al.* 2003; Tomasello & Carpenter 2005; Gómez 2007). That is, while great apes and humans may engage in morphologically similar behaviours (gaze following, gaze alternation, whole-hand pointing, etc.), the behaviours are underpinned by different psychological processes and/or motivations. Joint attention (versus joint attention *behaviours*) is widely defined as involving the mutual awareness that two or more individuals attend to a common focus, which is most convincingly demonstrated if one individual spontaneously initiates attentional contact with another. Controversy, however, remains about whether apes' initiation of attentional contact and subsequent production of pointing behaviours imply that they point in a truly referential way, and if pointing by captive apes represents a natural communicative capability, or a by-product of life in a human environment, including in a limited referential space (Tomasello & Call 1997; Leavens *et al.* 2005) where it represents a sophisticated form of (human) tool-use to attain object related goals. That is to say, whether the producer's half of the Gricean bargain is upheld, and the animals produce the gestures assuming that they carry a symmetrical meaning for signallers and recipients.

The present results add to the growing body of evidence suggesting that functional referential communication (i.e., signals that *function*, but are not necessarily *intended*, as referential signals: Crockford & Boesch 2003; Slocombe & Zuberbühler 2005, 2006) and seemingly

referential communication (i.e., signals that *both* function *and* are intended as referential signals: Pika & Mitani 2006) are a part of chimpanzee's intra-specific communicative repertoire. The finding that chimpanzees may use subtle and multi-modal cues to follow and direct others to distal locations, suggests that intra-specific ape 'pointing' may involve elements other than the arm, hand and index finger. Moreover, it provides the first systematic empirical evidence to support Menzel's (1973) suggestion that apes may engage in some form of inconspicuous body pointing. These observations accord with naturalistic observations of human infant pointing, which is typically combined with other gestures, gaze alternation and vocalisations (Zinober & Martlew 1985). Indeed, this form of chimpanzee manipulation of conspecifics may have been overlooked in previous studies because it is expressed through multiple and inconspicuous behaviours that may involve auditory behaviours, the head and the whole body, rather than a conspicuous, specialised (and consistently produced) referential signal, such as a hand or index finger point.

Apes engage in a variety of collective activities, including food sharing (e.g., Mitani & Watts 2001), coalitionary mate guarding (Watts 1998), territorial patrolling (Watts & Mitani 2001; Boesch & Boesch-Achermann 2002) and aggression (e.g., de Waal 1988), as well as consolation of victims of aggression and (based on anecdotal reports) treatment of injured individuals, suggesting that they engage in some form of empathy (Flack & de Waal 2000; Preston & de Waal 2002). Still, there is considerable evidence that they find it difficult to understand human cooperative pointing in food-finding situations (e.g., Herrmann & Tomasello 2006, though for recent positive results, see Lyn *et al.* 2009 and Mulcahy & Call 2009), and show little altruistic behaviour towards conspecifics when given the opportunity to costlessly provide them with food (Silk *et al.* 2005; Jensen *et al.* 2006). Overall cooperative ape behaviour is limited to mainly kin and reciprocating individuals.

That non-human apes do not engage in non-imperative pointing, such as informative and declarative pointing, has been interpreted as being underpinned by a lack of a cooperative desire to share information and experiences (e.g., Tomasello 2006). Non-imperative pointing does, however, not need to involve a cooperative motive. Individuals may direct others to distal locations, not to request an object, but to provoke an attentional and/or emotional reaction that they can use to discern ambiguity and provide information about how the subject should respond (termed 'social referential pointing' in Chapter 1). As detailed in Chapter 1, social referential pointing is neither about spurring others into action to obtain an object for the subject (imperative motivation), nor to express or share interest, or provide information (informative

pointing and high-level cognitive interpretation of declarative pointing), but to *provoke* an *attentional response* that the individual can use to guide its own behaviour and response. That is to say, one may point and direct others to distal locations for non-imperative, yet still selfish purposes. Such pointing, minimally, implies that individuals conceive others as having emotional and/or behavioural responses towards the environment that can be elicited by manipulating their attention.

The present design did not address the question as to whether the apes behaved to influence others' mental states (frequently interpreted to underlie a declarative motivation, e.g., Baron-Cohen 1989, 1995; Tomasello 1999, Liszkowski *et al.* 2004), or to evoke an attentional and/or emotional reaction as reflected in overt manifestations that could be used for social referential purposes (social referential motivation). The results for the chimpanzees were, however, overall consistent with both interpretations. Differentiating between the two motivations would have required that the target animals were allowed to actually detect (i.e., examine) the stimulus, so that the subjects' responses to the target animal's reaction to the stimulus could be examined. More specifically, the distinction would have required analysis of whether the subject appeared satisfied, if the conspecific simply looked to the stimulus and then engaged with the subject (i.e., declarative motivation, to simply *share* attention), or if the subject appeared to modify and adjust its behaviour towards the stimulus according to the valence of emotional response of the target (social referential motive). In the present design, however, the stimulus was removed before it fell within the visual field of the target animal (to preserve the novelty value of the stimulus, for targets who also served as communicators), thus preventing analysis of whether the subject modified its behaviour as a function of the other's response to the stimulus. In the light of past research, however, it seems reasonable to conclude that apes, under some circumstances, engage in social referential pointing, in which they direct conspecifics to hidden objects for 'selfish', interrogative purposes, so as to elicit an attentional response (as reflected in overt manifestations) that may be used to disambiguate the situation (see also Gómez *et al.* 1993). Future adaptations of the design would benefit from allowing targets would to actually look to and examine the stimulus. This would, however, require letting the animals serve as, *either* only communicator or only target (not both, as in the present design), and thus that the test be run with a considerably larger sample of subjects.

This interpretation is consistent with the claims by Bates and colleagues (Bates *et al.* 1975) that prior to actual declarative pointing, human infants engage in earlier types of declarative communication, including e.g., the showing of objects. Indeed, the frequently cited

anecdotal observation of a feral bonobo soliciting conspecifics to human researchers (which is typically given a [tentative] cooperative declarative interpretation) may, equally, be interpreted with reference to a (selfish) motive of calling others' attention, so as to ascertain how to respond to the discovery of ambiguous stimuli. It is also consistent with the observation by Menzel (1973) that chimpanzees led conspecifics to discover the location of e.g., novel toys, which might have been underpinned by fear of travelling alone, or a desire to ascertain how to respond.

9.5 Concluding remarks

Non-human primates almost invariably fail tests based on the cooperative object-choice task (Itakura *et al.* 1999; Call *et al.* 2000; Povinelli *et al.* 2000; Hare & Tomasello 2004). Recent research, however, has shown that the object-choices of lemurs are primed by the gaze cues provided in pictures of adult males from the animals' own groups (Ruiz *et al.* 2009). That is, when shown a picture of an adult male lemurs selectively chose the box upon which gaze of the individual in the picture was directed. Importantly, the study suggested that the failure of previous studies to find evidence that non-human primates successfully use others' gaze cues to make object choices, may owe to a failure to take into account the animals' overall low levels of gaze following. Intriguingly, the study suggested that data from many primate species are likely to show correct object-choices as a result of gaze following if the data are reanalysed (considering only the association between gaze following and object-choice in trials, in which subjects actually *follow* the model's gaze). In conjunction with the present finding that chimpanzees were more likely to follow the gaze of the dominant male of their group, this lends promise for future tests using the object-choice paradigm. It suggests that although the strong gaze following skills of many non-human primates have rarely translated into an ability to use others' gaze and gestural cues to locate hidden resources, primates may perform better on the object-choice task if the directional cues are provided by socially dominant members of their own species.

The results of this thesis suggest that chimpanzees, bonobos and orangutans followed the attention of conspecifics, and provide the first empirical support for Menzel's (Menzel 1973, 1974) suggestion that apes may include particular postural components to direct others' attention to novel objects in their environment. The results suggest that the paucity of reported instances of observed pointing behaviours in apes may owe to the inconspicuousness and multi-

faceted nature of the signals. Moreover, the overall results and anecdotal observations of mother-offspring dyad interactions suggest that the lack of evidence of 'social referential pointing' behaviours during interactions with humans does not necessarily equal evidence of lack ability to produce such during interactions with conspecifics, but that the cause may be partly motivational, and that such behaviours are more likely to occur between individuals with close emotional bonds. Perhaps important for the present results, the experiment removed possible constraints, such as competition and fear, by presenting a non-food stimulus of potential, but ambiguous, significance. The results suggest that the capacity to communicate about novel distal events during close-contact joint attentional episodes may have been present in the ancestor of the hominids and *Pan* species.

Overall, the results of the research presented in this thesis lends support to the growing body of evidence that suggests that although infant apes rarely coordinate attention between others and external objects (Bard & Vauclair 1984; Okamoto-Barth & Tomonaga 2006), juveniles and adults do (Pitman & Shumaker 2009; Tanner & Byrne 2010). Thus, while some controversy still remains in the literature, regarding apes' ability to share attention in a coordinated, triadic manner, the animals' behaviour in the present experiment, and in an extensive amount of reports involving different species and contexts (social games, bonobos: Pika & Zuberbühler 2008; gorillas: Tanner & Byrne 2010; tests of social referencing: Chimpanzees: Russell *et al.* 1997: repeated gaze alternation during imperative food-, object-, and action requests: Chimpanzees: e.g., Gómez 1996; Leavens & Hopkins 1998) suggests that apes are capable of some form of basic joint and coordinated attention.

Many conclusions regarding ape cognition and communication are based on the behaviour of a small number of repeatedly-tested animals in rather contrived laboratory settings. In the light of the growing body of evidence that suggest that apes engage in a number of collaborative and joint activities during less formalised and more dynamic contexts, such as e.g., play contexts, and indeed in contexts involving conspecifics, it seems that observing the animals during naturalistic interactions with conspecifics is a far more fruitful avenue for uncovering the true nature their abilities.

9.6 Proposed further research

9.6.1 Elaboration of present design

There are a number of avenues for expanding this research program. First, the use of a laser stimulus with an optical diffractive element that produces a biologically relevant image (e.g., animals or faces) is promising for further exploration of triadic interactions, as its display can be adapted to the animals' ranging patterns and locations, rather than requiring the positioning a stationary object and awaiting animal detection thereof. The nature of the experiment (requiring calm, interactions between the animals, without disturbance and potential indication as to the stimulus' location by the public) meant that many trials were abandoned, due to the arrival and/or disturbances from the public (during pre-stimulus phases). Moreover, the presence of a glass barrier separating the animals and the experimenter meant that the stimulus, when displayed through the glass at certain angles, produced a visible reflection on the glass itself. Opportunities to conduct trials where stimulus display to undisturbed participants remained covert were therefore rare. While a field application of the design would be complicated by issues, such as the poor visibility of dense forest vegetation, hampering identification of the locus of the animals' attention, the absence of human disturbance and glass barriers would facilitate the ease and speed, with which trials could be conducted.

Second, the effectiveness and seemingly intentional production of the 'hunch' in chimpanzee attention following contexts, calls for the experimental design to be adapted to examine the prevalence of this behavioural component in attention following contexts in wild chimpanzee populations. Third, the promising, but exploratory, study of the effect of social dominance on attention following in chimpanzees (reported in Chapter 4) requires further confirmation by a controlled study, using e.g., a focal animal sampling method.

Fourth, the procedure could be administered to species other than those examined in this thesis. I conducted pilot trials with individuals from number of additional species: captive gorillas (N = 2, three *experimental*, one '*Target and ignorant communicator*' and three '*No stimulus*' trials), wolves (N = 2, two *experimental* and two '*Target Alone*' trials), Diana monkeys (N = 8, 17 *experimental* and a number of '*Target Alone*' trials), Hamadryas baboons (*Papio hamadryas*), Hamlyn's monkey (*Cercopithecus hamlyni*), siamangs (*Symphalangus syndactylus*), leopards (*Panthera pardus*), capybaras (*Hydrochoerus hydrochaeri*) and meerkats (*Suricatta suricatta*). Siamangs and Hamlyn's monkeys were fearful of the stimulus, while leopards, capybaras and meerkats appeared to ignore it. Gorillas, Diana monkeys, baboons and wolves were promising candidates

for future studies, as at least one individual of each species engaged and played with the stimulus, and both gorillas and wolves seemingly referenced conspecifics upon seeing the stimulus. A simplified version of the design (involving three *experimental* and two '*Communicator Alone*' trials) has been administered to capuchin monkeys (G. Barclay, B.Sc. Thesis 2009), but produced no evidence of triadic interactions. Another simplified version is currently being adapted and conducted with chimpanzee mother-infant dyads in the field, to explore social referencing and triadic communication about the stimulus. Infant 'communicators' here receive the equivalent of an '*Experimental-facing away*' trial, and mothers and infants receive trials, in which the stimulus is presented to both, simultaneously. While the design lacks a number of controls implemented in the present design (e.g., '*Target Alone*'/'*Target and Ignorant Communicator*', '*No Stimulus*', 'pre-stimulus vs. stimulus phase control'), which complicates discrimination of chance behaviours and looks among infants and mothers, from behaviours evoked *by* and communicated *about* the stimulus, the study will contribute information about the prevalence of intra-specific social referencing, to evidence of this among human-raised chimpanzees and their caregivers (Russell *et al.* 1997).

9.6.2 The efficacy of different forms of deixis

9.6.2.1 Gestural pointing

Despite the prevalence of index finger pointing in the West, and the consequent typical inclusion of index finger extension in the definition of pointing, other morphological forms of deixis are prevalent, and in some cases dominant, in non-Western cultures. Experiments by Menzel (e.g., 1974) and results presented in this thesis suggest that chimpanzees may deploy behaviours other than hand and index finger extension to intentionally direct others to locations in the environment. Moreover, lip pointing (a quick shifting of the eyes towards an intended entity, and raising of the eyebrows and head, during which the mouth is first opened, and then closed with the lower lip thrust outward from the face: Wilkins 2003) bears some affinity with the 'chin pushed towards the stimulus' component of the 'hunching' posture observed in chimpanzees. It has been argued that other forms of deixis but index finger pointing are less efficient and precise (e.g., Hewes 1981; Butterworth 2003), yet there is little direct comparative evidence thereof. Indeed, the efficacy and precision of different types of pointing on human target localization have not been examined empirically. The proposed experiment is repeated measures design with five gesture types presented in each of two light levels (ambient and dim

light): (i) Gaze only, (ii) lip pointing, (iii) lip pointing without gaze, (iv) hand positioned close to chest, hand extended, (v) hand positioned close to chest, index finger extended. Numbered locations would be positioned on the floor in front of, and walls behind and to either side of a participant (Figure. 9.1). Participants would be required to determine, which of twenty-four numbered locations in four sections was indicated by the gestures.

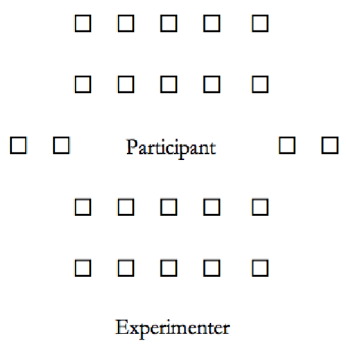


Figure 9.1: Experimental setup. The participant sits on a chair facing an experimenter, positioned 4m from the participant.

9.6.2.2 Vocal pointing

Visibility in rain forest habitats is generally poor and the acoustic domain thus represents a more effective means, than gestures, for communication between individuals beyond immediate proximity. The ability to direct the attention of others to objects and events in the environment using vocal stimuli ('vocal pointing') may therefore represent a more efficient means of attention manipulation for forest dwelling primates, than visual gestures (see also Gómez 2004). While sound localization acuity has been extensively studied, and is well established within a number of species (e.g., blackbirds, *Turdus merula*: Larsen & Dabelsteen 1990; chimpanzees: Kojima 1990; humans: see Middlebrooks & Green, 1991 for a review), no study could be found in the published literature that investigated discriminative abilities regarding the broadcast *direction* of sound (rather than its origin). The proposed experiment tests the hypothesis that humans are capable of directional auditory discrimination. If so, it opens the possibility that directional auditory sound *could* be deployed intentionally to direct others to outside entities.

The experiment is a repeated measures design with four levels: (i) stimulus type (the discrete sound 'ba' and continuous sound 'there' emitted for 3s by an experimenter), (ii) distance

between the experimenter and participant (4m, 6m and 8m), (iii) obstruction (none/foliage positioned 2m in front of the experimenter's face), (iv) sound direction (four directions relative to the participant (45°, 135°, 225°, 315°) at two angles (horizontally and at a 45° upward angle, Figure 9.2). Blindfolded subjects would wear headphones with white noise for 10s in between trials, to minimize the potential for direction judgements, made on the basis of volume comparisons across trials. Half of subjects would receive trials facing the experimenter, the other half while facing away from the experimenter. Subjects should receive a minimum of 20 trials in each condition, presented in a randomised order, and indicate the perceived sound direction by the raise of an arm. In an exploratory pilot with human subjects (N = 3), in which the two stimulus types were emitted in four horizontal directions from an unobstructed distance of 2.5m behind subjects, subjects correctly determined the direction of vocalising in 89 % (161 of 180) of trials. The results were promising, and the design has scope for adaptation to intraspecific studies of e.g., non-human primates, dogs and dolphins.

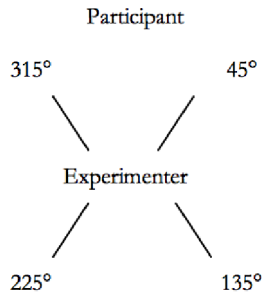


Figure 9.2: Broadcast directions and spatial alignment of a blindfolded subject and experimenter.

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APPENDICIES

Appendix 1: Images of outside chimpanzee enclosure (Twycross Zoo)

Appendix 2: Images of inside orangutan enclosures (Twycross Zoo)

Inside enclosure 1 at Twycross Zoo.

Inside enclosure 2 at Twycross Zoo.

Appendix 3: Bonobo and orangutan subjects used in some key studies

Table 1. Bonobos used in key studies. HR = hand-reared; MR = mother-reared. * = Excluded from test phase.

Investigators	Aim	Kuno HR	Limbuko HR	Joey HR	Ulindi MR	Yasa MR
Bräuer *et al.* 2005	Direct & Geometiric gaze following of humans	X	X	X	X	
Kaminski *et al.* 2004	Food begging from human in various attentional states	X	X	X		
Liebal *et al.* 2004	Ibid.	X	X	X	X	X
Okamoto-Barth *et al.* 2007	Gaze following through windowed & opaque barriers	X	X	X	X	X
Bräuer *et al.* 2005	Human point following	X	X	X	X	
Call 2007	Pointing to indicate selection	X	X	X	X	X
Zimmermann *et al.* 2009	Pointing to inform humans about a tool	X	X	X *	X *	X
Pele *et al.* 2009	Pointing to request object from conspecifics	X	X	X	X	

Table 2. Orangutans used in pointing experiments of Zimmerman *et al.* 2007 and Pele *et al.* 2009.

Species	Individual	Zimmermann *et al.* 2009	Pele *et al.* 2009
Orangutan	Dokana	X	X
Orangutan	Dunja	X	X
Orangutan	Padana	X	X
Orangutan	Pini	X	X
Orangutan	Toba	X *	
Orangutan	Walter	X *	
Orangutan	Bim		X